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STUDIES OF THE RETROCEREBRAL COMPLEX IN THE HONEY BEE[1] PART I: ANATOMY AND HISTOLOGY

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The corpora allata, corpora cardiaca, and structures associated with them can be appropriately termed the retrocerebral complex because of their location posterior to the insect brain. Since this complex has been studied only superficially in the honey bee, the following investigation was initiated to provide anatomical, histological and embryological bases for research in the almost virgin field of honey bee endocrinology. Anatomical and histological findings will be reported in this paper and the embryological development of the complex in a subsequent one.

MATERIALS AND METHODS

Both alcohol-preserved and living specimens of all casts were used. Since, aside from possible variations in size and development, the anatomy of the complex appeared the same in all casts, no designation was made as to whether specimens described were taken from drone, queen, or worker bees.

Dissections of living material were made in Levy's physiological solution with the help of a dissecting microscope and vital stains. The best vital stain was found to be methylene blue.

Prepared slides of serial sections were used to verify the gross findings and add histological and cytological detail. Various nuclear and cytological stains were tried. The best of these was phosphotungstic acid hematoxylin. Because of this stain's selective and deferential staining ability no counter stain was used after the developmental phases of the work. Iron hematoxylin with iron alum mordant was also satisfactory as a stain, but yielded less differentiation than did phosphotungstic acid hematoxylin.

Figures 2 and 3 are tracings of projected images from serial sections with details filled in by hand.

THE COMPLEX IN THE ADULT HONEY BEE

The corpora allata (3 of FIG. 1) are found laterad to the esophagus (10) They lie just below the centerline of the esophagus and their posterodorsal and inner surfaces lie nestled in a socket formed by the more superior and medial corpus cardiacum (2) of each side. In the honey bee each corpus allatum is joined to the corresponding corpus cardiacum not by a nerve, but rather by a broad band of tissue to be described later.

The corpora cardiaca are conspicuous bodies lying primarily dorsomedially to the corpora allata. They are much more elongate, and as a result, extend somewhat more anteriorly than do the corpora allata.

The paracardial nerves (5) are not divided into two branches as in many insects, but rather, are single stocky nerves joining each corpus cardiacum with the corresponding lobe of the tritocerebrum (13).

A distinct ring of neural and aortal tissue surrounds the esophagus at the level of the allata. This ring is made up of two structures which arise from the corpus cardiacum of one side and extend, one (4) dorsally and one (7) ventrally, across the esophagus to the opposite corpus cardiacum. As far as can be determined, these prominent structures (to be termed the paracardial commissures) have not been described previously in any insect.

The position of the tissue just described makes possible neural communication in three different planes. This arrangement suggests analogy to the semicircular canals of the vertebrates and thus suggests a possible function of this ring of tissues in the honey bee—that of the maintenance of equilbrium. Heymons (1899) suspected the corpora allata to be involved in this function, but demonstrated that this was not so, at least in Bacillus sp. (Orthoptera). Nevertheless, equilib-

[1]A portion of a dissertation presented in partial fulfillment of the degree of Doctor of Philosophy at Ohio State University. The author would like to express his appreciation to Dr. Winston E. Dunham of Ohio State University, under whose guidance this study was made, for his valuable advice and assistance.

rium in insects is still largely unexplained and this complex offers investigators another approach to the problem.

The recurrent nerve (6) extends posteriorly along the dorsal wall of the esophagus and then bifurcates into two branches (the esophageal nerves) which proceed posteriorly through the neck region while associated with the lateral surfaces of the esophagus. This bifurcation occurs slightly caudad to the paracardial commissures, and it is also somewhat posterior to the pharyngeal suspensor ligaments (11) which extend from the posterior limit of the pharnyx to the dorsal wall of the head capsule. These pharyngeal supporting "ligaments" of Snodgrass (1925) are actually muscular in nature and thus possibly may function as posterior pharyngeal dialators as well as being sustentative structures.

Both Cazal (1948) and Rehm (1939) state that the hypocerebral ganglion (*id.* occipital ganglion, and the esophageal ganglion of Snodgrass, 1935) of the recurrent nerve is absent in the honey bee. However a noticeable swelling of the recurrent nerve was observed in four of the specimens examined (less than 2%). This enlargement occurred in the region where a hypocerebral ganglion might be expected if present, *i.e.*, just anterior to the bifurcation of the recurrent nerve. When adults were sectioned and studied microscopically, many had a greater number of neuron cell bodies in this region than in adjacent areas. This leads to the question: Is a hypocerebral ganglion really absent in the honey bee "and other higher Hymenoptera—other than Formis", as stated by Cazal, or is it just reduced and thus only inconspicuously present in this group? Further work could be done to check the latter possibility as it seems to be more descriptive of the actual condition in the honey bee.

It can be seen from Figure 1 that the aorta or dorsal vessel (9) is closely associated with the retrocerebral complex. It has been noted by several authors (Nelson, 1924, *et al.*), that the aortal vessel anteriorly becomes a floorless structure with the shape of an inverted "U" (8). According to the literature this transition from tube to trough and the anterior termination of the aorta occur at some ambiguous place "anteriorly". It was found that the dorsal paracardial commissure ventrally, the corpora cardiaca laterally, and the cardiacal bridge (1) dorsally mark the anterior limit of the aortal vessel in this insect (1, 2, 4, 8 of FIGS. 1, 2, 3). It would be interesting to determine whether or not this holds true for other species as well. Because there is a definite anterior terminus to a formerly indefinitely described structure, and because blood is conveyed anteriorly beyond this point by an inverted epithelial trough in which it is contained ventrally by the tissues of the esophagus, it would seem plausible to suggest that the aortal vessel conducts blood anteriorly into a true sinus (8 of FIGS. 1, 3). This aortal sinus then conducts blood anteriorly through the circumesophageal commissures and thence into the haemocoele proper.

Tracheation of the complex was not studied in great detail. However, the branches of the anterior thoracic trunks, which pass anteriorly along either side of, and very close to the corpora allata, give rise to air sacs and small branches which are abundant in the region of the complex (12 of FIG. 3). Deroux (1948) states that the corpora allata of Odonata are penetrated by minute trachea. Microscopic examination of these tissues in the honey bee did not demonstrate this tracheation in either the corpora allata or corpora cardiaca.

THE CORPORA ALLATA OF THE HONEY BEE IN DETAIL

Historical

Müller first observed the insect corpora allata in 1828 and since then these bodies have been studied in numerous insects. Possibly the best treatise on the anatomy of these bodies is that by Nabert (1913), which covers the general anatomy of these structures in many species of insects, including the honey bee. Nabert also published a photomicrograph of a section through the head of the honey bee at the level of the corpora allata, and described the anatomic relationships of the corpora allata in some detail. A few of these details have not been verified in this study.

Pixell-Goodrich (1920) published the only account in the English language of the adult honey bee structures and included one diagram which depicts a spherical body, in the approximate region of the corpora allata, apparently mislabelled the "esophageal ganglion". His description, stating that "these occur one on each side of the esophagus as it emerges from between the supra- and sub-esophageal ganglia—that is, these are just in front of the commissures", is misleading. Apparently, he is referring to a larval structure which fuses into the subesophageal ganglion in the adult.

In a rather sizable treatise on bee anatomy, Betts (1923) mentions the corpora allata as being "120 microns in diameter" but gives no figures or further details. Nelson (1924) in his study on the larval bee states that the "corpora or so-called 'ganglia' allata as they are well known now, have no intimate connection or relationship with the nervous system". Snodgrass (1925) does not mention or diagram the corpora allata. Rehm (1939) is the only writer other than Nabert to deal somewhat accurately with the anatomy of this complex in the honey bee. He describes the location of the allata in a general way, and he, too, states there is no direct connection between them and the nervous system. Pflugfelder (1948) and Hanström (1942) made some observations and

drew conflicting conclusions on the size of the corpora allata of the three casts of honey bee.

Adult Anatomy

The location of the corpora allata has already been discussed. For all practical purposes each is subspherical in shape and seems to "float" in its normal position. No clear-cut structures of suspension are present although there is a tendency for the more medial hemisphere of each body to be buried in the exterior epithelial cells of the esophagus and, more dorsally, in the neural and aortal cells of the corpora cardiaca (FIG. 2).

The size of these structures appears highly variable. Adult allata varied in diameter from 60 microns to about 130 microns with the usual size being approximately 90 to 100 microns. An insufficient number of specimens was measured to yield statistically valid results. From a preliminary standpoint, the published reports on size in relation to sex or age variations appear contradictory. Further work should be done along this line before any attempt is made to utilize present data concerning the size of the corpus allatum in the honey bee.

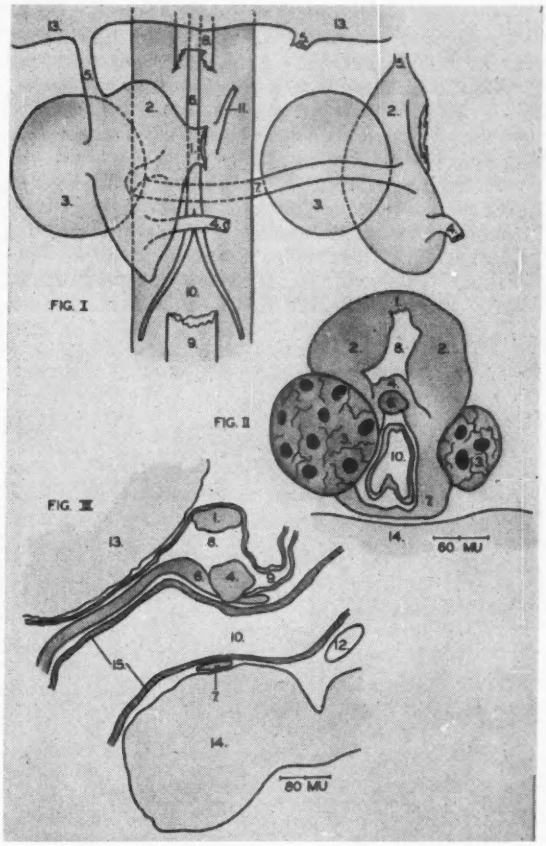
The corpus allatum is innervated, not by a clearcut nerve from the corpus cardiacum as is the case in many forms, but rather by a diffuse band of fibers that extends downward from the more dorsal corpus cardiacum, through an inconspicuous connection between the two bodies, and into the corpus allatum (FIG. 1). Here the neural fibers appear to spread out more or less fan-like and lie primarily near the surface of the corpus allatum.

Adult Histology and Cytology

The allatal body proper is covered with an inconspicuous membrane (A of FIG. 4). The origin of this membrane has not been studied, although it is possible, based upon the origin of the allatal cells proper, that this corresponds to the basement membrane of the body wall.

The approximately 80 to 100 distinctive cells that comprise the adult allatal tissue appear to be typically secretory (epithelial) cells. They are approximately 2½ times the diameter of the nucleus which measures 12 to 15 microns in diameter. These cells are arranged somewhat loosely but enclose only a little extra-cellular space. Cell membranes are indistinct and fragmentary, but not absent in the adult as some previous investigators (Nabert, 1913, *et al.*) thought. When iron hematoxylin is used as the nuclear stain, cell membranes do stain very weakly or not at all and their obscureness plus this resistance to staining may explain the difference in observations. Unlike the cell membrane, the nucleus absorbs stain well. This is also true of the nuclear membrane.

Since the allatal cells are all approximately the same size, and since they are arranged somewhat



EXPLANATION OF THE NUMBERS USED ON THE FIGURES

1. Bridge between the two corpora cardica.
2. Corpus cardiacum.
3. Corpus allatum.
4. Dorsal paracardial commissure.
5. Paracardial nerve.
6. Recurrent nerve.
7. Ventral paracardial commissure.
8. Aortal sinus.
9. Aorta
10. Esophagus.
11. Either (right or left) esophageal suspensor ligament.
12. Branch of the anterior thoracic tracheal trunk.
13. Brain.
14. Subesophageal ganglion.
15. Wall of the esophagus.

FIGURE 1. Diagramatic relationship of the structures in the retrocerebral complex. This is a dorsal view with the anterioposterior distance slightly lengthened. Structures on the left are in their normal position; those on the right have been detached dorsally and rotated to the right.

FIGURE 2. Slightly oblique cross-section of the complex at the level of the corpora allata. Shown are the histological relationships of the corpus cardiacum (2), corpus allatum (3), aortal sinus (8), esophagus (10), and the dorsal and ventral paracardial commissures (4, 7).

FIGURE 3. Longitudinal-section of a typical complex. Shown are the relative positions of the cardiacal bridge (1), aorta (9), aortal sinus (8), esophagus (10), and the dorsal and ventral paracardial commissures (4, 7).

uniformly throughout the body, their centrally located nuclei are more or less evenly distributed in the body itself. It is this rather even distribution of extremely large, deeply staining nuclei, each of which is surrounded by a very darkly staining nuclear membrane that gives the tissue its characteristic appearance (FIG. 4).

Rather angular and exceptionally large granules which take up nuclear stains very heavily are scattered about among the rather dense, but small, evenly distributed granules of the nucleoplasm. The tendency for these nuclear granules to be more noticeable in the larval nuclei than

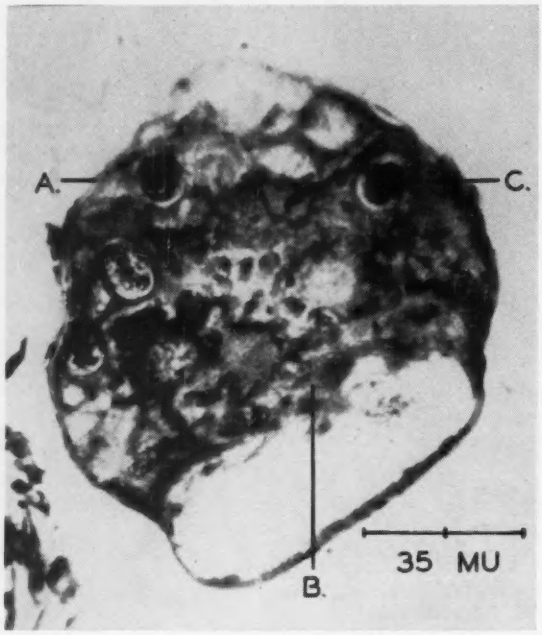


FIGURE 4. Corpus allatum of an old field worker. Note the allatal membrane (A), the nuclear membrane (B), and the dense nucleus (C).

in the nuclei found in older stages has led Zee and Pai (1944) to describe the corresponding nuclei of *Chironomus* as pycnotic. If this term does not necessarily imply a degenerative process, it very well describes the appearance of the larval nucleus and to a lesser extent that of the old adult as well. Occasionally a still larger, deeply-staining object can be found within the nucleus which is apparently crystalline in nature. These objects remain unexplained at the present time.

THE CORPORA CARDIACA OF THE HONEY BEE IN DETAIL

Historical

The corpora cardiaca appear to be as universally present in adult insects as are the corpora allata. However, literature on these bodies is extremely scattered except for a dissertation by Cazal (1948). According to Hanström (1942), the corpora cardiaca were described for the first time by Lyonet in 1762.

In an article on the honey bee, Rehm (1939) mentions that corpora cardiaca are present. Whether or not he was referring to the bee is not clear, since just before and after this statement he was definitely referring to structures as they are found in insects in general. So far as could be determined, except for a brief description as to their location and general shape by Nabert (1913) in his paper on the corpora allata of insects including the honey bee, and the mention of the structures by Rehm (noted above), there is no other information concerning the corpora cardiaca of the honey bee.

Nabert mentions that the pharngeal gland (*i.e.*, corpora cardiaca) in this insect is paired and located dorsal to the esophagus. He states also that these structures are innervated from the brain and are united with one another dorsally. The rest of his description with respect to the honey bee is somewhat vague or even in error.

The corpora cardiaca are not mentioned in the treatises on honey bee anatomy and morphology by Snodgrass (1925), Nelson (1915), (1924), Pixell-Goodrich (1920), or Betts (1923).

Adult Anatomy

Each corpus cardiacum lies just posteriorly and ventrally to the tritocerebrum and parallel to the dorsolateral surface of the esophagus. Each resembles superficially a half pear with the convex surface upward and the larger portion anterior. Nabert pointed out that the two bodies fuse with each other. This connection occurs dorsally and anteriorly, thus forming a bridge over the aortal cavity below (FIGS. 1, 2). In the adult honey bee the corpora cardiaca appear almost as conspicuous as the corpora allata both in the stained and unstained condition and it is surprising they have been overlooked by so many anatomists.

Except for the bridge, the posterior and anterior margins as well as the medial margin abruptly become thin. These margins are continuous with the epithelium of the circulatory system (FIG. 3). Ventrally each corpus is discontinuous tissue except where it gives rise to the commissures previously mentioned and where each connects with the more lateral and ventral corpus allatum.

Adult Histology and Cytology

The corpora cardiaca are covered with epithelial tissue which is continuous with that of the aorta. Scattered irregularly throughout the bodies are moderately sized ovoid nuclei measuring 3 to 4 microns in length.

Each corpus cardiacum is composed of a neuroglea-like mass made up of a blending of neural and

aortal tissues. These two tissues blend and intermix into a typical neural tissue which for lack of better designation will be called insect neuroglea. Its function has not been demonstrated but its appearance, anatomic relationships, and its ability to absorb certain differential stains such as methylene blue and not gentian violet indicate that structurally the corpora cardica are probably a neural complex.

Two distinct regions appear in the corpus cardiacum. These differ in the proportions of aortal and neural tissue that compose them. The anterior ventral fourth (approximately) of the corpus is made up of a mixture of neural and circulatory tissue in which neural fibers are the more abundant. It is a region which appears denser and which takes a deeper stain than does the posterior larger portion of the cardiacum. This anterior portion is also the region into which the fibers of the paracardial nerve initially pass after breaking away from their conspicuous tract that enters the lower anterior portion of the corpus.

The posterior three-fourths of the corpus is also made up of the same two tissues but here the neuroglea consists of a lighter staining, more spongy type of tissue which apparently is largely of circulatory origin.

So far as is known this is the first time that two regions have been observed or described with respect to this structure in any insect. It will be interesting to determine whether these two regions are found generally in insects, as slides[2] of *Blatta orientalis* have since demonstrated them to be present in this cockroach also.

THE PARACARDIAL COMMISSURES OF THE HONEY BEE IN DETAIL

These heretofore undescribed linear structures (4, 7 of FIG. 1) are found communicating between the two corpora cardiaca. One of these structures lies dorsad to the esophagus; the other, ventrad. Because of this arrangement, these shall be designated the dorsal and ventral paracardial commissures.

Each commissure is made up of neurogleal tissue of a spongy appearance and each, like the corpus cardiacum, is covered by a thin layer of circulatory epithelium in which are numerous cells with ovoid nuclei. The ventral commissure extends between the two corpora from points about midway on their medial surfaces. It passes under the esophagus at a point just anterior to the transverse tentorial bar of the head. As it extends downward, it gradually becomes less cylindrical until, at its extreme ventral position, it is ovate or even thickly ribbon-like. At this point it measures about 6 x 20 microns.

[2]Prepared and graciously shown the writer by Dr. W. C. Myser of Ohio State University.

The dorsal commissure is shorter, larger, and remains irregularly cylindrical throughout its length. It extends between the corpora from points slightly to the rear and in some cases above the origin of the ventral commissure, and passes upward and over the esophagus. At its thickest, it almost completely encloses the recurrent nerve (FIG. 2). Never was much space found between its lower surface and the outer margin of the esophagus.

Although the dorsal commissure appears to lie in close contact with the recurrent nerve, it should be noted that in only one doubtful case was a nerve present that appeared to link the retrocerebral complex through the dorsal commissure to the recurrent system. For this reason, though contrary to the original working hypothesis which was based on information primarily from other insect orders, a direct neural link between the retrocerebral and recurrent systems seems to be lacking in the honey bee.

Histological and anatomical differences which are related to the embryogeny and post-embryogeny of this complex will be treated in a later paper.

SUMMARY

1. Two histologically different regions in the corpora cardiaca of an insect are described.

2. Two previously undescribed structures, the dorsal and ventral paracardial commissures, are recorded in the literature on honey bee anatomy.

3. The gross and minute anatomy of retrocerebral complex of the honey bee is described and observations are made on its histology.

4. A comment is made as to the structure and anterior terminus of the circulatory vessel of the adult honey bee.

5. Observations on the honey bee have suggested the re-examination of present concepts concerning the presence or absence of the hypocerebral ganglion in Hymenoptera.

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UTILIZATION OF VARIOUS PRODUCTION MEDIA BY MUSCOID FLIES IN A METROPOLITAN AREA. II. SEASONAL INFLUENCE ON DEGREE AND EXTENT OF FLY PRODUCTION[1]

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U. S. Department of Health, Education, and Welfare, Phoenix, Ariz., and Atlanta, Ga.

In a previous paper, the authors reported sources of muscoid fly production and species occurrence in the Phoenix, Arizona, area, but omitted reference to amounts of media infested, the production potential of naturally occurring substrates, and seasonal factors which influenced the availability of the media. As these considerations are of significance in the control, as well as the investigative, aspects of a fly abatement program, they serve as a basis for the present report.

METHODS

The general technique of surveillance and the sampling pattern were the same as described in the previous paper. (Siverly and Schoof, 1955.) To obtain the additional data necessary for this report, certain field observations were recorded at the time the infested substrate was examined. Essentially, these involved an estimation of the amount of medium infested and the degree of infestation therein. The cubic foot was used as the unit for estimating the volume of the infested medium, and degree of infestation was classified as follows:

Larvae Per Quarter Pint of Medium	Classification
1–10	Light
11–20	Moderate
>20	Heavy

Code numbers were assigned to 21 different types of media; by the use of these numbers and the code letters signifying degrees of infestation, the field inspector could readily record the essential information on the form sheet. A numbering system was used to identify each field record with a specific block in the study area.

For the analysis of the data, an arbitrary formula was devised to express the over-all degree of infestation in fly-breeding media. By application of this formula, the 3 levels of infestation can be expressed as a single measurement "production index." Factors of 1, 3, and 9 were arbitrarily selected to represent the 3 classes of infestation—light, moderate, and heavy. Application of the formula when 50, 30, and 20 cubic feet of light, moderate, and heavily infested media were detected is shown in Table 1. This same index can also be used as a measure of production potential of specific substrates.

TABLE I

Derivation of Fly Production Index for Media Utilized. Phoenix, Arizona, 1951–52.

Classification	Factor		Amount Infested (Cu. Ft.)		
Light.....	1	X	50	=	50
Moderate...	3	X	30	=	90
Heavy.....	9	X	20	=	180
			100		320

$$\text{Index} = \frac{\Sigma \text{ Factor X Amount Infested}}{\Sigma \text{ Amount Infested}} = \frac{320}{100} = 3.2$$

RESULTS

A seasonal breakdown of the observed amounts of infested media is shown in Table 2. These estimated amounts are shown in whole numbers.

[1]Accepted for publication Sept. 29, 1953.
[2]Now at Oregon State College, Corvallis.

For purpose of simplification, the 7 different types of animal excrement are lumped into one category, and scattered and contained garbage are considered under the single heading "Garbage." The figures pertaining to the miscellaneous category represent totals from several different types of media, each too infrequent in its incidence to warrant specific inclusion. However, certain of these media are of special seasonal significance and will be discussed later.

The point of particular interest in Table 2 is the shift in the intensity of fly breeding in all three categories from light to heavy in the time transitions between spring and fall. At the same time, proportionately more media were observed in the moderate to heavy categories as the seasons advanced. Winter conditions permitted fly development, but the trend was toward light infestations.

The data in Table 3 are derived in part from Table 2. Since the number of block inspections differed for the individual time periods, this variable was eliminated by expressing the volume of infested media in terms of cubic feet observed per block inspection. The findings indicate an inverse relationship exists between amounts of available media and the "production index" during the spring, summer, and fall seasons. Apparently the decrease in the amount of available breeding materials results in increased competition for those substrates still present and thereby concentrates the foci of infestation.

The degree to which individual substrates are utilized for fly breeding may well be a yardstick for estimating their respective productive potentials. Such data are presented in Table 4. As the findings show, there is considerable difference in the extent to which each of the various media was utilized. Under excrement both pig and chicken excreta possessed indices well above the general average for that class of media. Likewise, melons reflected a much higher index than any other substrate. Infestations detected in melons were chiefly heavy concentrations, whereas other substrates were characterized by varying degrees of fly breeding.

The data which show scattered garbage to be less abundant and less productive than garbage in containers require further explanation. Al-

TABLE II

DEGREE AND EXTENT OF FLY LARVAL INFESTATIONS DURING FOUR SEASONS AT PHOENIX, ARIZONA, 1951–52

MEDIA	MARCH-APRIL MAY CUBIC FEET INFESTED				JUNE-JULY-AUGUST CUBIC FEET INFESTED				SEPT.-OCT.-NOV. CUBIC FEET INFESTED				DEC.-JAN.-FEB. CUBIC FEET INFESTED			
	Light	Mod.	Heavy	Total	Light	Mod.	Heavy	Total	Light	Mod.	Heavy	Total	Light	Mod.	Heavy	Total
Animal excrement....	1350	1737	79	3166	100	1122	552	1774	6	52	1186	1244	1537	331	325	2193
Garbage.....	86	58	16	160	<1	58	85	143	<1	8	48	56	7	56	15	78
Miscellaneous*.	107	92	36	235	12	12	36	60	4	13	31	48	42	12	6	60
Total.....	1543	1887	131	3561	112	1192	673	1977	10	73	1265	1348	1586	399	346	2331

*Grass clippings, dishwater wastes, coffee grounds, melons, dead animal, stock feeds, vegetables, etc.

TABLE III

SEASONAL INFLUENCE ON AVAILABILITY AND UTILIZATION OF FLY BREEDING MEDIA. PHOENIX, ARIZONA, 1951–52

MEDIA	SPRING		SUMMER		FALL		WINTER	
	Cu. ft. inf. per block inspection	Production index	Cu. ft. inf. per block inspection	Production index	Cu. ft. inf. per block inspection	Production index	Cu. ft. inf. per block inspection	Production index
Animal excrement...	13.5	2.30	7.6	4.75	4.4	8.71	4.1	2.49
Garbage.....	0.6	2.54	0.6	6.53	0.3	8.16	0.2	3.95
Miscellaneous.....	0.9	3.01	0.3	6.21	0.3	6.72	0.1	2.14
TOTAL.....	15.0	2.36	8.5	4.93	5.0	8.62	4.4	2.53

though not obvious from the figures, the findings support garbage collection practice and emphasize the seriousness of scattered garbage as fly breeding media. It is estimated that less than 20 percent of the garbage cans were infested. This estimate is based upon independent surveys conducted during the summer and fall of 1951. In a June survey of approximately 10 percent of the residential blocks, 2.6 percent of the cans in the survey blocks were found positive for breeding. In November, a similar survey revealed infestations in 6.0 percent of the cans. In each coverage, more than 1900 garbage cans were inspected. Surveys were also conducted in a lower middle-class housing project over a 12-week period from May to September. Out of 729 garbage can inspections, 124 or 17.0 percent revealed infestations. Since the housing project was practically devoid of other fly production media, the results might be considered extreme, and not representative for all residential areas.

TABLE IV

FLY LARVAL INFESTATIONS IN VARIOUS MEDIA. PHOENIX, ARIZONA, 1951–52

MEDIA	TOTAL CUBIC FEET INFESTED	PRODUCTION INDEX FOR MEDIA UTILIZED
Animal Excrement		
Cow	815	2.07
Horse	1865	2.63
Chicken*	5511	4.46
Dog	12	3.10
Rabbit	124	3.43
Pig	44	7.09
Garbage		
Scattered	185	4.53
In container	253	5.02
Miscellaneous		
Grass clippings	191	2.68
Dishwater†	10	5.02
Coffee grounds	40	2.52
Melon	23	8.87
Stock feed	17	5.74
Other (dead animals, meat, bones, seafood, wastes)	127	....
TOTAL	9217	3.87

*The data indicated for chicken excrement should not be interpreted as a conclusion that this medium was the most important source of flies in the city. The vast amount of excrement is due largely to samples from one chicken ranch on the city border.

†Denotes moist soil impregnated with organic matter present in "dishwater" waste.

In contrast, the infestation rate of scattered garbage is much higher, and is likely to exceed 50 percent of the available media. Moreover, there appears to be an increased tendency for *M. domestica* to utilize scattered garbage more readily than contained garbage. Although storing the garbage *per se* obviously does not eliminate the fly breeding problem in that medium, it is evident that if all garbage were scattered, the rate of infestation would more than double and the resulting breeding potential, considering the bulk of available media, would be tremendous.

DISCUSSION

As the results show, inverse relationships exist between the amounts of media infested and the production index for spring, summer, and fall (table 3). In general, fly breeding in the Phoenix area is most readily observed during the spring months when conditions are most favorable for fly development. In 1951, monthly temperatures for March, April, and May averaged 70° F. and the mean relative humidities were in the 40 to 50 percent range. With the onset of summer, there was a sharp rise in temperature and a corresponding drop in relative humidity. Many of the media which were exposed to the sun (excrement, in particular) underwent rapid dehydration and no longer supported fly production. Dessication, rather than high temperatures, was the limiting factor for fly breeding during the season, since media with a relatively high water content, such as waste melons and contained garbage, continued to be foci for fly production. In small animal pens, fly breeding was most frequently observed in the vicinity of watering troughs, where spilled water contributed the necessary moisture to sustain the larvae in the medium. Further illustration of the significance of moisture is afforded by the unprecedented heavy rains in late August, 1952 which provided sufficient moisture to large areas of cattle droppings to permit copious fly production in this medium. Previously, the substrate was devoid of infestation except at sites adjacent to watering troughs. As the high temperatures ensuing the rainfall were of similar magnitude to those previously present, moisture, rather than temperature, appeared to be the critical factor suppressing fly production.

During fall, the fly breeding appeared to be even more concentrated than in summer. This state is somewhat puzzling since environmental conditions simulated those present during the spring months, although the relative humidity was slightly higher. Observed fly densities approximated the spring peak, a result of the abnormal rainfall in August. However, only about 20 percent of what appeared to be production media actually was utilized. Possibly, with diminishing light hours and a gradual decrease in mean temperatures, adult female flies were not stimulated to oviposit except in very selected areas. In the relatively few sites where fly breeding was observed, the media were generally heavily infested.

During the winter period, monthly average temperatures were 50 to 55° and relative humidities reached their highest levels (50 to 60 percent). The amounts of infested media approached those observed during the fall season (Table 3) but the degree of infestation was much lower. Considering all factors, and in particular temperature, the winter period was the least favorable for fly production. Many of the larvae collected in the field were in the prepupal (quiescent) stage, and actual emergence was observed primarily at selected sites where the media were exposed to direct sunlight. Thus on a seasonal basis, limited moisture retards fly production in the summer whereas in the winter the low temperature is the critical factor inhibiting fly development.

By combining the "production index" and the amount of infested material per block inspection, it is possible to compare the fly breeding potential in the sample blocks for the seasons of the year. The respective product values for spring, summer, fall, and winter were 35.4, 41.9, 43.1, and 11.1. These figures bear no significance *per se;* they are valid only as comparative indices. Such a collation indicates that sustained fly production occurred in the sample blocks throughout the year, the intensities for spring, summer, and fall being similar and as a group distinct from that of the winter period. Some significant comparisons may be drawn between this pattern of fly breeding and that of observed adult activity. The pattern for adult activity is analogous, except for summer. Extremely high temperatures during this season may be as inhibitory for fly activity as are low temperatures in winter. Whereas during winter, adult activity is characteristically a state of semi-hibernation, adult activity in the hot summer period approaches a state of semi-aestivation except during the cooler early morning hours. The fact that adult density levels during winter are below those of midsummer is probably due to the lowered temperature—more critical as an inhibitory developmental factor than moisture deficiency. Moist substrates, although limited in their extent, are still available in selected locations during summer; in winter, cool temperatures prevail generally, and retardation of the developmental cycle may prevent emergence of any great magnitude.

A primary peak of adult activity is usually evidenced in Phoenix during the spring. (Savage & Schoof, unpublished.) "Seed" foci which persist through the winter season together with optimum weather conditions are responsible for this primary peak. A secondary peak of adult activity usually occurs in the fall. Since in the fall environmental conditions are less favorable for fly production than in the spring, this secondary peak of adult activity presumably reflects, in larger measure, breeding foci established during the summer. Therefore, control measures which are specifically directed toward elimination of breeding sites may, in an area where fly control is essentially a year-round problem, inversely yield the highest return during the seasons of lowest adult fly densities.

Since the horse-and-buggy era, fly breeding has been associated with horse excrement. Even today there is still a common impression that that particular medium excels in fly production potential. Under certain conditions, this may be true. However, in comparison with other excreta observed on this study (Table 4), horse excrement was only more heavily infested than cow excrement and less so than the other types, particularly pig excrement. These observations agree with those of Thomsen and Hammer in Denmark (1936), who rated pig, horse, and cow excrements in that order as fly breeding substrates. Rabbit excrement, although not often referred to as a ready source of fly production, can serve as a prime focus for fly infestation in residential areas where other excrements are of infrequent occurrence or even in situations where ample competing substrates exist.

Field observations substantiated the general concept that practically any warm, moist, putrescible material can support muscoid fly production. Excrement (particularly when it contains spilled feed), garbage, stock feed, and melons serve as potent sources of fly production. By tests with known numbers of larvae, it has been shown that these media can provide sufficient sustenance to allow larval development at the rate of one cubic centimeter of substance per fly. On that basis, one cubic foot of infested media will develop more than 28,000 flies; one average-sized cantaloupe can produce at least 1,000 flies. Garbage exposed to ovipositing flies has produced as many as 70,000 flies per cubic foot which indicates an even higher rate of yield than one fly per cubic centimeter.

Grass clippings present a seasonal fly problem in the Phoenix area since many residents utilize rye grass for their winter lawns. Customarily they sprinkle or inundate their lawns with water to stimulate growth. If the lawn clippings are piled when wet, they soon begin to decompose and form a medium—not unlike certain animal wastes—which constitutes an important source of fly breeding in the better class residential areas.

The indiscriminate dumping of melon culls and waste lettuce in the fringe area around the city has imposed a serious fly problem in the community during certain months of the year. Although the impact of these disposal practices upon the community fly problem is temporary, the magnitude of the infiltration of flies into the municipality is such that basic remedial measures must be designed. The influx of fly migrants is intensified by the limited period that the wastes

are attractive to flies, since once the media become desiccated, the flies are forced to disperse elsewhere for suitable breeding conditions.

A comparison of breeding potential for the seasons of the year was discussed previously. This comparison was based upon product values derived from "production index" and amounts of infested media. The same method can be used in the determination of the relative importance of the different media as sources of fly infestation in the community. By such application (Table 4), the rank order of importance for the various types of media is as follows: (1) chicken excrement, (2) horse excrement, (3) cow excrement, (4) contained garbage, (5) scattered garbage, and (6) grass clippings.

However, it is obvious that any particular type of substrate, even though high in production potential, may be relatively insignificant if limited in its natural occurrence. Commercial enterprises—one chicken ranch and two large racing stables—were responsible for most of the chicken and horse excrements. Cow excrement was found most frequently in rural blocks within the area, whereas garbage and grass clippings were media associated with strictly residential sections of the city. Thus the greater prevalence of residential blocks within the city augments the relative importance of those substrates (garbage and grass clippings) in contributing to the fly problem of the community. Small scattered foci, because of area involved and the increased number of individual landowners to contact, frequently outweigh in control significance the more prolific fly production sites of limited and localized occurrence. Before assigning priorities to the various breeding problems, the control supervisor must consider these factors, as well as the dispersal range of the fly and the availability of legislative aids and policies relating to environmental sanitation.

It is apparent that the results described from the present study would vary to a degree with the yearly changes in environmental conditions. Nevertheless, the findings provide a guide in evaluating the fly breeding problem not only in the southwest but in municipalities elsewhere in the country. It is obvious that house flies are opportunists that quickly capitalize upon man's indiscretion in handling animal and plant wastes. A recognition of this adaptability and the reproductive potential of *Musca domestica* is essential to the accomplishment of sustained effective fly control.

SUMMARY

Larval surveys at Phoenix, Arizona, for a 12-months period in 1951–52 indicate that fly breeding is sustained throughout the year. During the spring, summer, and fall seasons, an inverse relationship existed between the amounts of various media infested and the degrees of infestation. Summer infestations were concentrated in those substrates of relatively high moisture content or were subject to a moist environment. Winter conditions permitted imaginal development but the magnitude of fly production was inhibited by low temperatures.

Assignment of values 1, 3, and 9 to light, moderate, and heavy infestations provides a "production index" whereby the degrees of fly infestation can be quantitatively compared during four seasons. The "production index" can also be used as an indication of the breeding potential of the individual substrates. Chicken and pig excrements, garbage, melons, and stock feed displayed the highest fly production potentials.

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UTILIZATION OF VARIOUS PRODUCTION MEDIA BY MUSCOID FLIES IN A METROPOLITAN AREA. III. FLY PRODUCTION IN RELATION TO CITY BLOCK ENVIRONMENT[1]

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In the two previous papers in this series (Siverly and Schoof, 1955), information was reported relevant to the sources of production for different species of muscoid flies, and seasonal influence upon degree and extent to which the media were utilized. This paper discusses the relationship between these production sources and block environment.

Few, if any, cities of 100,000 population can be considered as homogeneous in composition. The various sections of the city may differ sufficiently from each other so as to be designated by such broad terms as "high-class residential" or "middle-class residential." Within the individual sections, arbitrary lines can be drawn which define areas of stricter homogeneity. The unit area most uniformly affected by insanitary conditions within its boundaries—and hence, generally the most homogeneous—is the city block. Since city blocks provide a narrower range of environmental conditions than do the more comprehensive categories, a considerable gamut of sociosanitational levels may be represented by 1000 or more block areas. Therefore, any assumption that all blocks contribute equally to a municipal "fly condition" is entirely unwarranted.

METHODS

In establishing this study, it was necessary to classify the block types upon the criteria of sociosanitational factors. The categories adopted were as follows:

Type I —Blocks with a high standard of premises sanitation, twice-weekly pickup of garbage, animal shelters absent except possibly dog houses, no commercial establishments.

Type II —Blocks with good premises sanitation, *twice-weekly pickup of garbage*, occasional rabbit or chicken pens or business establishments.

Type IIIa—Blocks with poor premises sanitation, *garbage collection infrequent* or lacking, animal pens common.

Type IIIb—Blocks with poor premises sanitation, *garbage collection adequate*,[3] animal pens common.

Type IV —Blocks with scattered residences, rural in nature, animal pens common, without garbage collection or with limited service.

Type V —Dump blocks (hog farm, dairy, horse stables, etc.)

Type VI —Blocks composed primarily of business establishments (daily pickup of garbage).

The study area was composed of approximately 1,500 blocks. The 116 blocks which were selected as survey stations represented approximately an 8 percent sample. The number of blocks in each category and the frequency of block inspections are shown in Table 1.

TABLE I

BLOCK CATEGORIES AND FREQUENCY OF INSPECTION

BLOCK TYPE	NUMBER OF BLOCKS IN CATEGORY	NUMBER OF BLOCK INSPECTIONS
I	8	69
II	49	443
IIIa	5	42
IIIb	27	227
IV	8	79
V	8	92
VI	11	94
TOTAL	116	1046

Other details of the survey procedures were reported in the two preceding papers of this series.

RESULTS

The estimated amounts of fly production media as they relate to block type and season are shown in Table 2. For the purpose of simplification, cow, horse, chicken, dog, sheep, rabbit, and pig excrement were considered under the general heading of excrement, while scattered and contained garbage were listed as garbage. Twelve different substrates, such as grass clippings, dead animal, vegetables and stock feed, which are relatively minor in significance when considered individually, were classed in aggregate under miscellaneous. Since certain block types were surveyed more frequently than others, this variable was eliminated by expressing the volume of infested media in terms of cubic feet observed *per block inspection*.

As Table 2 reveals, the amounts of miscellaneous media infested for Type I blocks during the spring season exceeded comparable values for all other block types. This condition was attributed to the piles of infested rye grass clippings which prevailed throughout the better class residential blocks. Winter lawn grass, although common in the Phoenix area, is cultivated to the greatest extent by the more affluent homeowners.

[1]Accepted for publication September 29, 1954.
[2]Now at Oregon State College, Corvallis.
[3]Twice-weekly garbage pickup was maintained in study blocks.

The detection of 2.4 cubic feet of infested excrement in Type I blocks during the spring season is somewhat anomalous; by definition, this block type did not contain animal pens. However, certain homeowners utilize animal excrement for fertilizing their winter lawns. One inspection showed an estimated 30 cubic feet of infested horse manure on a newly cultivated lawn and flower bed of an elite residence. Obviously, the beautiful exterior appearance of such a premises does not negate its consideration as a potential source of fly production.

The point of differentiation between Types IIIa and IIIb blocks is the frequency of garbage collection. As would be expected, greater quantities of infested garbage were detected in the Type IIIa blocks. It should also be noted that more than three times as much infested excrement was found in the Type IIIa blocks. This condition was due in part to the higher incidence of animal pens in such blocks. In addition, kitchen wastes from homes in these areas were commonly fed to chickens. As these wastes frequently possessed a high water content, they provided good fly attractants and also increased the suitability of the excrement as a potential medium for fly breeding.

Animal excrement was observed to be the principal source of fly infestations in both the rural (Type IV) and dump blocks (Type V). Where much of the block was taken up by pasture and no great concentration of animals was evident, the block was characterized as Type IV. Dump blocks (Type V) were extremely high in fly potential and required special surveillance and control applications. In circumstances where animals were the contributing factor in the classifying of a block as Type V, the animals were concentrated and usually maintained as a business enterprise. The eight Type V blocks represented 2 horse stables, 2 dairies, 1 hog farm, 1 pony rides concession and small zoo, 1 mental institution, and 1 block with several acreages. With the exception of the pony rides concession, these blocks were within the city limits.

With reference to the business blocks (Type VI), it is noteworthy that comparatively small amounts of garbage were infested. Considering the quantities of garbage produced from food-handling establishments in the business area, the low rate of infestation is indicative of the efficacy of daily garbage pickup in prevention of fly breeding conditions.

In general, the data in table 2 indicate that fly breeding was most prevalent in spring but existed to a certain extent in practically all block types during all seasons. Since numerous

TABLE II

ESTIMATIONS, IN CUBIC FEET PER BLOCK INSPECTION, OF INFESTED PRODUCTION MEDIA IN THREE CATEGORIES, ON A BLOCK TYPE AND SEASONAL BREAKDOWN. PHOENIX, ARIZONA, 1951–52.

MEDIA	SPRING (March-May)	SUMMER (June-Aug.)	FALL (Sept.-Nov.)	WINTER (Dec.-Feb.)
I				
Excrement	2.4	<1	<1	0
Garbage	<1	<1	<1	<1
Miscellaneous	5.5	<1	<1	<1
II				
Excrement	2.7	<1	<1	<1
Garbage	<1	<1	<1	<1
Miscellaneous	<1	<1	<1	<1
IIIa				
Excrement	3.3	<1	<1	<1
Garbage	2.2	<1	<1	1.9
Miscellaneous	<1	<1	<1	<1
IIIb				
Excrement	<1	<1	<1	<1
Garbage	1.1	<1	<1	<1
Miscellaneous	<1	<1	<1	<1
IV				
Excrement	30.5	4.2	2.0	7.6
Garbage	<1	<1	<1	<1
Miscellaneous	<1	<1	0	<1
V				
Excrement	135.3	101.4	64.9	48.7
Garbage	<1	1.6	<1	<1
Miscellaneous	3.2	<1	<1	1.0
VI				
Excrement	<1	<1	0	0
Garbage	<1	<1	<1	<1
Miscellaneous	<1	<1	<1	<1

media are not suitable to fly production in the summer period chiefly because of moisture deficiencies, these minor infestations can assume major significance whenever rainfall occurs. The normal production potential of these substrates, coupled with the adaptability of the flies to utilize such media, augments the significance of these "seed" foci.

Table 3, which is derived in part from table 2, depicts the total amounts of media infested on a seasonal basis. The greater amount of infested material reported for Type I block in comparison to Types II and IIIb is due principally to the seasonal prevalence of grass clippings as discussed on page 325. Points of distinction between Type II and Type IIIb blocks concern the more common occurrence of animal pens and poorer premises sanitation in blocks in the latter category. The fact that amounts of infested media

TABLE III

INFESTED PRODUCTION MEDIA PER BLOCK INSPECTION, ACCORDING TO BLOCK TYPE AND SEASON. PHOENIX, ARIZONA, 1951–52

SEASON	BLOCK TYPE							
	I	II	IIIa	IIIb	IV	V	VI	MEAN*
Spring	8.4	4.1	5.7	2.1	32.0	139.0	1.3	15.0
Summer	1.0	1.1	1.9	1.6	4.6	103.5	0.8	8.5
Fall	0.5	0.4	1.2	0.3	2.0	65.7	0.4	5.0
Winter	0.1	0.1	2.4	0.8	7.7	50.0	0.3	4.4
Yearly index	2.5	1.4	2.8	1.2	11.6	89.6	0.7	8.2

*Since dump blocks (Type V) received inspections more frequently than other type blocks, the mean has been adjusted according to formula

$$\frac{\Sigma \text{ number of blocks in category} \times \text{cubic feet media per block inspection}}{\text{number of blocks surveyed (116)}}$$

were equal or were less in the IIIb category may be attributed to the degree of sanitary effort directed at the potentially significant sources of fly production in these blocks by the local fly control program. Observed fly densities were consistently higher in the Type IIIb blocks because of the presence of the animals and other attractants. However, the mere existence of these pens may not be as significant from the standpoint of fly breeding as the manner in which the animals are maintained and the clean-up practices employed.

The mean index of infested media by volume decreased in the time transitions from spring to winter. However, despite the progressive decline, there were significant quantities observed at all seasons of the year in both residential and dump blocks (table 4). Dump blocks of the type surveyed exhibit a fly potential of tremendous magnitude. Based on an estimated 90 cubic feet of breeding media and a production potential of 28,000 flies per cubic foot of infested substrate, a block of such makeup could produce in excess of 30 million flies a year, even if the developmental cycle extended to one month. This is a conservative estimate, since certain media have been observed to produce as high as 70,000 flies per cubic foot, and *Musca domestica* may produce as many as 18 generations per year in the Phoenix area.

DISCUSSION

The importance of sanitation in municipal fly control has been strongly emphasized by recent workers (Coffey and Maier, 1950; Maier and Baker, 1951; Scudder, 1949). In practice, this fundamental principle depends for its application upon a background of factual information obtained from survey data. As Quarterman *et al.* (1949), point out, the relative importance of the various fly breeding sources varies with local

TABLE IV

COMPARISON OF ESTIMATED CUBIC FEET OF PRODUCTION MEDIA IN SURVEY RESIDENTIAL AND DUMP BLOCKS ON A SEASONAL BASIS. PHOENIX, ARIZONA, 1951–52.

SEASON	CUBIC FEET INFESTED PER BLOCK INSPECTION	
	RESIDENTIAL*	DUMP STATIONS
Spring	6.3	139.0
Summer	1.5	103.5
Fall	0.6	65.7
Winter	1.0	50.0
Entire Year	2.4	89.6

*Indexes of volumes infested in Types I, II, IIIa IIIb, and IV blocks combined.

conditions, and each city should be the subject of a thorough survey by competent observers in advance of attempting municipal fly control.

The data obtained from this survey underline the necessity for consideration of local conditions. Phoenix, for example, has increased in population by more than 50 percent in the last decade. Concomitant with this rise in population, the city has extended its boundaries and now encompasses block areas which a few years ago were small farms. As a consequence, many of these rural blocks are now surrounded by new residential developments. Although the maintenance of farm animals on these so-called rural blocks invites criticism from surrounding city dwellers, the owners of livestock rest their case upon prior habitation and seek to maintain their animals.

In recognition of the livestock owners' point of view, city officials usually are reluctant to institute legislation which would abolish such animal pens until neighborhood opinion is

strong enough to make the livestock owner's position untenable. However, the problem is by no means insolvable. A clean-up stipulation in the city ordinance can serve as the intermediate step. Frequently the resident elects to eliminate his animals rather than comply with the clean-up regulations. Ultimately, problems of this type solve themselves as residential dwellings gradually encroach to such an extent that the farm owner finally retreats to less populated zones.

The same evolution prevails in relation to dump blocks. Most of these establishments now located in the center of residential areas are on sites which formerly were on the periphery of the urbanized zone. Remedial measures again include ultimate elimination, preceded and aided by adequate legislation.

The problem of animal pens or dump blocks in this study area illustrates a local condition which, although generally more common in the southwest, can and does occur in remaining sections of the country. Survey data, by providing factual information relative to the nature and location of such blocks, are basic to an intelligent and successful approach to the problem.

The reported data reveal that rural (Type IV) and dump (Type V) blocks provided a much greater fly potential than did the other block types. Essentially, this is a reflection of the abundance of animal excrement in such blocks. However, it must be emphasized that the data (tables 3 and 4) should not be considered as portraying the exact status of the different block types in creating the fly problem in the city.[4] As previously indicated (page 326), the 8 dump blocks surveyed represented the majority of such blocks within the city whereas the survey samples of the other block types composed only a relatively small proportion of the total number of these blocks within the community. Consequently, because blocks of Types I-IV and VI are greater in number within the city, they contribute more significantly to the local problem than is implied by the survey data. Broadly speaking, the problem of fly breeding in a municipality classifies into two categories: (a) sites of heavy fly production potential but few in number, and (b) sites of low fly production potential but frequent in occurrence. An example of category (a) is a chicken ranch dump station located at the city limits of Phoenix. This one establishment contained a greater volume of fly breeding media than all of the residential survey blocks in the city combined and produced an output of flies that reached astronomical figures. The importance of a problem site of this type is further augmented by the wide dispersal range of *M. domestica*. Dispersion tests in Phoenix have revealed that marked flies released at two dump blocks roamed freely over the urban area. Thus, it is obvious that any control program must give immediate and consistent attention to these "hot beds" of fly production. Close cooperation with owners of problem establishments to effect remedial changes in plant operation often results in successful abatement. However, it is only through adequate surveillance of the breeding area that effective and feasible corrective recommendations can be devised.

An illustration of the problem posed by sites in category (b) is found in the fly production in grass clippings. During the spring period, grass wastes accumulate behind the majority of the dwellings in the better class residential sections. Since this product falls under the rubbish category, removal of grass clippings was frequently delayed for 3 to 4 weeks. By calling the conditions to the attention of the city officials, improved facilities for rubbish pick-up during the critical spring period resulted and the problem was eliminated.

Of greater significance to the community fly problem than seasonal items is household garbage. Large amounts of this medium are seldom encountered, yet the ubiquitous occurrence of garbage in a city magnifies its significance. Obviously, garbage can surveys, such as those described in the second paper of this series, should be included in the over-all fly breeding survey. Results of these surveys provide a basis for promotion of recommended household practices in garbage storage, such as wrapping the garbage and storing it in cans of sufficient capacity with tight-fitting lids. When such practices are employed, fly breeding in garbage can be kept within reasonable limits of control.

While breeding surveys serve as a necessary prerequisite and guide to effective community fly control, the general scope of surveillance for the average municipal program need not be as detailed as in the present study, which was designed for research purposes. The chief requirements are suitably trained personnel, adequate coverage of the city, critical appraisal of the results, and then application of the same to the control operations. How completely these requirements are fulfilled is contingent upon the community involved. Regardless of the thoroughness employed, however, the basic fact remains that to cope successfully with any problem, the fundamental causes must be known—in fly control, this signifies knowledge of the type, magnitude and distribution of the fly breeding sources.

[4]Throughout the present study, independent fly control operations in the city were focused toward elimination of breeding sources so that the present data do not characterize conditions existing in an untreated municipality.

SUMMARY

During 1951–52, fly breeding surveys were conducted at Phoenix, Arizona, in 116 blocks

representative of 7 different block types. The latter were based on sanitational criteria and ranged from high class residential blocks to dump sites (dairies, chicken ranch).

Amounts of infested media were at the highest levels during spring (March-April-May) and progressively declined during the remainder of the year. Although fly breeding appeared to be generalized throughout the area, block types showed considerable variance in production potential as indicated by estimated volumes of infested media observed. Business blocks on a daily garbage collection pick-up schedule contained less infested media than any other block type. About twice the volume of infested media was observed in blocks where garbage collection was lacking in comparison to those blocks where garbage collection was adequate. Blocks with scattered residences, rural in nature, with animal pens, contained up to 9 times the volume of infested media found in other residential blocks.

Dump blocks were characterized by extremely high fly production potentials. On the basis of cubic feet of infested medium per inspection, the yearly index for dump blocks was 89.6 as compared to 2.4 for residential blocks.

Fly breeding surveys are recommended as a basic approach to the achievement of effective community fly control.

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DETOXIFICATION OF DDT IN RELATION TO CYTOCHROME OXIDASE ACTIVITY IN RESISTANT AND SUSCEPTIBLE HOUSE FLIES[1]

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The complex nature of the problem of insect resistance to insecticides has recently given an impetus to a wide variety of investigations along lines of insect morphology, physiology, behavior, and genetics. As a result of this voluminous work (a great part of which is as yet unpublished) it has become increasingly evident that resistance to one or more insecticides in various insect species and among strains of a single species cannot be characterized by a single common factor.

In the case of DDT-resistance in the house fly, *Musca domestica* L. it has been shown by Sternburg, Kearns, and Bruce (1950) and by Perry and Hoskins (1950) that DDT-resistant strains of flies are able to convert DDT into the relatively non-toxic derivative 2, 2-bis (*p*-chlorophenyl) –1, 1-dichloroethylene (DDE). This finding led some workers to conclude that detoxification is a major factor in DDT-resistance. Evidence in support of this conclusion was given by Perry, Fay, and Buckner (1953) who showed a correlation between detoxification of DDT and survival in several strains of DDT-resistant flies, and by the recent isolation from resistant houseflies of an enzyme, dehydrochlorinase, which is capable of dehydrochlorinating DDT *in vitro* (Sternburg, Vinson, and Kearns, 1953). On the other hand, Busvine (1951), concluded that, although dehydrochlorination of DDT could account for the resistance of his Sardinian strain of house flies, his Italian strain relied mainly on an unknown defense mechanism. Furthermore, the Italian strain exhibited marked resistance to knock-down by DDT (Harrison, 1952). This phenomenon could not be attributed to more rapid dehydrochlorination since Winteringham, Loveday, and Harrison (1951) found this strain to metabolize DDT very slowly. Thus it appeared that the two strains must possess somewhat different resistance mechanisms. Fletcher (1952) and Babers and Pratt (1953) reached similar conclusions, i.e., that the ability to metabolize injected DDT was not sufficient to explain the resistance of their respective strains of house flies.

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Another approach to the problem of DDT-resistance in house flies was the finding that DDT partially blocked a vital metabolic pathway, cytochrome oxidase, and this inhibition might be associated with alterations of essential physiological processes (Sacktor, 1949; Johnston, 1951). Subsequent investigations by Sacktor (heretofore unreported) with a purified soluble cytochrome oxidase preparation showed that after incubation with DDT for 1 hr. in the cold (0–3° C.) the rate of oxidation of reduced cytochrome *c* was diminished 50 percent. In addition to this inhibitory effect it was also observed that adults of a resistant strain had more cytochrome oxidase and that pupae of this same line had less of this enzyme than did a susceptible strain (Sacktor, 1950, 1951). Furthermore, these resistant pupae respired to a greater extent via an alternative system. Thus the results suggested that DDT-resistance in this strain might, in part, be correlated with the ability to maintain essential energy yielding processes despite partial inhibition of cytochrome oxidase. This hypothesis has now been further explored by comparing the cytochrome oxidase activity of several resistant and susceptible strains.

It also had been suggested that degradation of DDT to DDE might involve oxidation-reduction processes such as would be mediated by the cytochrome system (Sacktor, 1951; Chadwick, 1952). The present investigations are concerned with this possible relationship between the detoxification of DDT and the cytochrome oxidase activity in several strains of house flies.

METHODS

Pupae of the various fly strains were exchanged weekly for a period of seven weeks in order to make simultaneous tests with flies from the same culture and of the same age. The following strains were used in this study:

(1) *NAIDM—1948*—a susceptible laboratory strain
(2) *Control*—a susceptible laboratory strain
(3) *Beltsville*—a susceptible strain obtained from the U. S. D. A., Beltsville, Md.
(4) *Roberds*—a multiple resistant strain obtained from a dairy in Savannah, Ga.
(5) *DDT-45*—a DDT-resistant strain selected from the NAIDM—1948 strain
(6) *DMC—5*—derived from the DDT-45 strain by selection with space sprays containing DDT and DMC
(7) *Edgewood*—selected from the original Ellenville resistant strain
(8) *Urbana*—a resistant strain obtained from the University of Illinois
(9) *Orlando*—a resistant strain obtained from the U.S.D.A. at Orlando, Florida
(10) *Illinois "S"*—a slightly resistant strain obtained from the University of Illinois.

The Edgewood and Control strains were reared at the Medical Laboratories, Army Chemical Center, and the other strains were reared at the Communicable Disease Center, Savannah.

Dehydrochlorination of DDT was measured at Savannah as follows: Groups of fifty flies from each strain and sex were anaesthetized with CO_2 and 6.8 micrograms of *p, p'*-DDT in benzene were applied topically to the ventral thoracic region of each fly by means of a microloop. Two hours after application the flies were rinsed with three successive 15 ml. portions of n-hexane to remove the unabsorbed DDT. At this time the flies were ground in a mortar with anhydrous sodium sulfate and extracted with carbon tetrachloride by mechanical agitation for one hour. The extract was filtered off and the filtrate was evaporated to approximately 10 ml. and chromatographed through a Celite-sulfuric acid column (cf. Davidow, 1950). DDT and DDE were determined by the Schechter-Haller colorimetric method (Schechter, *et al.*, 1945).

The cytochrome oxidase activity of each strain and sex was determined at Edgewood by assaying, per shipment, five batches consisting of ten flies each. The flies were homogenized in 5 ml. of cold 0.03M phosphate buffer, pH 7.4, for one minute. The homogenate was then strained through gauze pads to remove gross particles. Immediately before the experimental run an aliquot of the stock homogenate was diluted 5-fold. The enzyme's activity was measured spectrophotometrically according to the technique previously described (Sacktor, 1950, 1952). To 2.9 ml. of the buffered reduced cytochrome *c* mixture was added 0.1 ml. of the diluted fly homogenate. Optical density readings were taken every 20 seconds for 3 minutes. Afterwards, in order to oxidize the cytochrome *c* solution completely, 0.1 ml. of 10^{-2}M potasium ferricyanide was added.

RESULTS

The recoveries of DDT and DDE, which are averages of seven determinations for male and female flies of each strain, are shown in Table 1. The total recovery in each determination was at least 92 percent of the applied dose. The amount of DDT absorbed represents, in each case, the observed quantities of internal unchanged DDT and of DDE. The percentage of DDT converted to DDE is calculated on the basis of DDT absorbed. It is evident that the susceptible strains, designated as NAIDM, Control, and Beltsville, metabolized little or no DDT whereas the resistant strains converted from 50 to 70 percent of the absorbed DDT into DDE. The Illinois "S" strain, presumably highly resistant to DDT, proved to be only slightly resistant as indicated by the low conversion of absorbed DDT and the high mortality.

It is also worth noting that there were significant differences in absorption of DDT among the various strains as indicated by the ratios of absorbed to applied DDT (Table 1). The three susceptible strains absorbed relatively large

quantities of the applied DDT, but so did the highly resistant DDT-45 strain and the moderately resistant Roberds strain. On the other hand, although relatively small amounts of DDT penetrated some of the very resistant strains this was not different from the low absorption also noted in the slightly resistant Illinois "S" strain.

The cytochrome oxidase activity of each strain, both male and female, is shown in Table 2. The results show that some strains differ in oxidase activity. The susceptible strain designated as Control has the least oxidase activity

Table 1 that the conversion of DDT to DDE in these strains is a contributory factor in the defense against the lethal action of DDT. The relative significance of this factor, however, varies with each strain. For example, the Roberds strain detoxified as large a percentage of the absorbed DDT as did some of the other resistant strains, yet it suffered greater mortality. Also, the slow initial rate of dehydrochlorination in some resistant strains (Busvine, 1951; Winteringham, Loveday, and Harrison, 1951) indicates that perhaps other mechanisms predominate in certain strains.

TABLE I

ABSORPTION AND METABOLISM OF DDT IN TWO HOURS AND PERCENTAGE MORTALITY IN 24 HOURS RESULTING FROM TOPICAL APPLICATIONS OF 6.8 MICROGRAMS OF DDT PER FLY

FLY STRAIN	SEX	RECOVERED (micrograms per fly)				RATIO ABSORBED TO APPLIED DDT	PERCENT ABSORBED DDT CONVERTED to DDE	24-HOUR MORTALITY (percent)
		External DDT	Internal		Absorbed DDT+DDE			
			DDT	DDE				
BELTSVILLE	M	6.21	0.55	0	0.55	0.08	0	100
	F	5.95	0.82	0	0.82	0.12	0	100
NAIDM	M	5.20	0.98	0.06	1.04	0.15	6.1	100
	F	5.05	1.13	0.07	1.20	0.18	6.2	100
CONTROL	M	5.63	0.67	0.04	0.71	0.10	6.2	100
	F	5.45	0.86	0.03	0.89	0.13	3.6	100
ILLINOIS "S"	M	6.26	0.33	0.05	0.38	0.06	13.2	90
	F	6.29	0.33	0.07	0.40	0.06	17.5	81
ROBERDS	M	5.12	0.48	0.65	1.13	0.17	57.3	38
	F	4.96	0.56	0.67	1.23	0.18	54.4	14
EDGEWOOD	M	5.97	0.15	0.20	0.35	0.05	57.3	9
	F	6.01	0.16	0.20	0.36	0.05	56.0	3
ORLANDO	M	6.34	0.12	0.13	0.25	0.04	50.6	6
	F	6.30	0.11	0.13	0.24	0.04	54.5	2
URBANA	M	6.05	0.16	0.22	0.38	0.06	58.4	9
	F	6.11	0.16	0.19	0.35	0.05	55.4	3
DDT-45	M	5.48	0.22	0.60	0.82	0.12	73.3	11
	F	5.52	0.25	0.52	0.77	0.11	67.3	3
DMC-5	M	5.85	0.09	0.35	0.44	0.06	79.0	5
	F	6.00	0.11	0.26	0.37	0.05	70.5	3

but the Beltsville susceptible strain, as well as some of the resistant lines, has the greatest. The other susceptible strain, NAIDM, although relatively low in oxidase activity, is not statistically different in this respect from some of the resistant strains. Therefore, it is not possible to distinguish all resistant strains from the nonresistant on the basis of cytochrome oxidase activity.

DISCUSSION

The present results emphasize the complex nature of DDT-resistance. It is evident from

Another factor in resistance which heretofore has not been fully investigated is the rate of absorption of the insecticide. The results of Table 1 clearly demonstrate significant differences in absorption among the strains studied. It is to be expected that a slow rate of absorption coupled with ability to detoxify the insecticide might contribute to a greater extent toward the apparent resistance of a strain by protecting such flies from accumulating a lethal dose.

It is also evident (Table 2) that some strains vary in cytochrome oxidase activity. Although a significant difference in oxidase activity between

the susceptible strain, (Control), and the resistant strain, (Edgewood), is still apparent (cf. Sacktor, 1950) it is now clear that there is no distinction in this respect between all resistant and non-resistant strains. The present oxidase experiments can be related to the studies of Fullmer and Hoskins (1951) who found no difference in the normal oxygen uptake of a resistant and a susceptible strain of flies, and to the work of Pratt and Babers (1953) who found that of the resistant strains studied, i.e., Edgewood, Orlando (Beltsville) and Bellflower, only the Edgewood strain had a significantly greater oxygen uptake than did the susceptible strains. Thus the hypothesis that resistant adults can maintain essential physiological processes despite partial inhibition of cytochrome oxidase cannot be attributed in all strains merely to a greater oxidase content. Whether it is a factor in some resistant strains, such as Urbana, Edgewood, and Roberds, has yet to be established.

TABLE II

CYTOCHROME OXIDASE ACTIVITY OF THE FLY STRAINS

FLY STRAIN	ACTIVITY*	
	Female Mean ± S.E.	Male Mean ± S.E.
BELTSVILLE	.312 ± .007	.212 ± .004
ILLINOIS "S"	.310 ± .007	.213 ± .004
URBANA	.281 ± .006	.247 ± .009
EDGEWOOD	.236 ± .006	.237 ± .008
ROBERDS	.239 ± .007	.222 ± .008
ORLANDO	.225 ± .010	.211 ± .009
DDT-45	.234 ± .006	.205 ± .007
DMC-5	.222 ± .006	.216 ± .008
NAIDM	.227 ± .006	.207 ± .009
CONTROL	.192 ± .005	.179 ± .007

*Activity expressed as $\frac{\triangle \log \text{ [Cytochrome c]}}{\triangle \text{ t (min)}}$

n = 35. Significant difference at 1 percent level is 0.024 and 0.027 for females and males, respectively.

There appears to be no direct correlation between detoxification and cytochrome oxidase activity in all the strains tested. As shown in Table II the susceptible strain (Control) has the least cytochrome oxidase activity and correspondingly shows the least detoxification of DDT. In contrast with this positive correlation, the other susceptible strains possess as much oxidase activity as do some of the resistant strains, but, as shown (Table I) do not detoxify DDT to any large extent. Thus, if there is any relationship between these two processes, its demonstration must await further clarification of the enzymatic nature of DDT breakdown in various strains of resistant house flies.

The mechanism of DDT detoxification has not yet been fully determined. There is evidence of the accumulation of degradation products other than DDE in some resistant fly strains (Tahori and Hoskins, 1953). Unknown breakdown products of DDT, designated in the literature as non-Schechter-Haller metabolites, have also been reported in the milkweed bug (Ferguson and Kearns, 1949), in the American roach (Vinson and Kearns, 1952; Butts, Chang, Christensen, and Wang, 1953) and in the Mexican bean beetle, the red-banded leaf roller, and two species of grasshoppers (Sternburg and Kearns, 1952). This suggests that the breakdown of DDT to its end products in the different insect species and fly strains might involve more than one step and might proceed through the mediation of more than one enzyme. Thus, in the present experiments, the failure to obtain correspondence between DDE formation and cytochrome oxidase activity does not necessarily preclude a possible relationship between DDT degradation and the cytochrome system in all species and fly strains.

In elucidating the mechanism of DDT-resistance, one must be cognizant of its multiple-factor character. Some of these factors may be cited as follows: Detoxification of DDT into known and unidentified metabolites by several possible enzymatic schemes; rate of absorption of the insecticide; the ability to maintain essential physiological processes in the presence of the toxicant at the site of action; the ability otherwise to withstand internal unchanged DDT in quantities sufficient to kill susceptible flies, as for example, by storage in non-sensitive tissues; shifts in behavior patterns which enable the flies to avoid the toxicant or minimize their likelihood of accumulating a lethal dose. The present studies indicate that a combination of several of these factors is responsible for DDT-resistance and further emphasize the probable interdependency of some of these factors. Moreover, these results suggest that each strain possesses a combination of attributes for resistance which may be different from that found in other strains.

SUMMARY

Ten fly strains, susceptible and DDT-resistant, were examined for their ability to convert DDT to DDE, to absorb DDT, and for their cytochrome oxidase activity. It was found that:

(1) The susceptible strains metabolize little DDT whereas the resistant strains convert absorbed DDT to DDE. The relative significance of this factor varies with each strain.

(2) Some strains differ in the rate of absorption of topically applied DDT.

(3) Some strains differ in cytochrome oxidase activity but no distinctions can be made in this respect between all resistant and susceptible strains.

(4) There is no direct relationship between cytochrome oxidase activity and degradation of DDT in all strains.

It may be concluded that DDT-resistance among all strains cannot be characterized by a single common factor. This study indicates that a combination of several factors is required and suggests that each strain possesses a combination of attributes for resistance which may be different from that found in other strains.

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THE SPIDER GENERA ORONOTA AND STEMMOPS IN NORTH AMERICA, CENTRAL AMERICA AND THE WEST INDIES (ARANEAE: THERIDIIDAE)

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The genera reviewed in this paper are two of many groups of comb-footed spiders believed to be closely related to *Theridion*. These genera have heretofore been placed in different subfamilies. Although Simon (1892) expressly stated that he used artificial characters for his separation of the Theridiidae into subfamilies, most arachnologists have followed Simon's classification for lack of a better one. Archer (1950) recently attempted a revision of the Theridiidae, using as a basis for his divisions, more modern characters such as detailed anatomy of the palpus. While I am not here attempting to present an improvement of Archer's system, which does not appear to be entirely satisfactory either, there is abundant evidence that only a careful study of the male and female genitalia, particularly an examination of the shape of the embolus and the position and attachment of the various sclerites in the expanded palpus, will show some of these relationships. The eye arrangement, shape of the carapace, and abdomen are, however, of considerable aid in defining genera. Sometimes these latter characters are more conservative than the genitalia and are a better superificial indication of these relationships. An examination of one of the Australian species of *Oronota*, for instance, demonstrated in the

prosoma and opisthosoma a surprising similarity to the American species. On the other hand, the palpus appeared quite different, indicating at first another genus. However, upon expanding the palpus by a short immersion in hot ten percent sodium hydroxide, it was found that a mere shift in the position of the embolus and slight changes in the shapes of various sclerites resulted in a superficial difference in appearance.

The present revision was made possible by the help, advice and the generous loan of spiders by Dr. W. J. Gertsch, Curator of Spiders of the American Museum of Natural History. Dr. R. V. Chamberlain of the University of Utah, Mr. H. Dybas of the Chicago Natural History Museum, and Dr. B. J. Kaston of the Teachers College of Connecticut at New Britain supplied additional specimens on loan. Dr. P. J. Darlington of the Museum of Comparative Zoology sent paratypes of *Stemmops darlingtoni* and Prof. L. Fage of the Muséum d'Histoire Naturelle of Paris sent cotypes of *Epeira paradoxa*. Dr. V. V. Hickman of the University of Tasmania, at Hobart, helped with the gift of some Australian *Oronota*. I extend thanks to all these, as well as to my wife, for help in writing this paper, and to Mrs. C. Crocker for library help.

The palpi illustrated are the left ones. The types of the new species have been deposited in the American Museum of Natural History.

Oronota Simon

Oronota Simon, 1871, Ann. Soc. Ent. France (5) 1: VII. Genotype: *Epeira paradoxa* Lucas, 1846.

Ulesanis L. Koch, 1872, Die Arachniden Australiens p. 242. Genotype: *Ulesanis personata* L. Koch, of Samoa.

Oroodes Simon, 1873, Mem. Soc. Roy. Sci. Liége (2) 5:127. Genotype: *Epeira paradoxa* Lucas, 1846.

Stegosoma O. P.-Cambridge, 1873, Proc. Zool. Soc. London p. 126. Genotype: *Stegosoma testudo* O. P.-Cambridge, of Ceylon.

Sclerogaster Cavanna, 1876, Boll. Soc. Ent. Ital. 8: 89. Genotype: *Sclerogaster pusillus* Cavanna (= *O. paradoxa* Lucas).

Heribertus Keyserling, 1884, Die Spinnen Amerikas, Theridiidae 2: 27. Genotype: *Heribertus rubromaculatus* Keyserling, of Brazil (Synonymized with *Ulesanis* by Simon).

Small theridiid spiders in which the head portion of the carapace is produced into a rounded lobe projecting high above the clypeus and bearing the eyes. Eyes subequal in size, and about equally spaced, except for laterals which are touching each other. Clypeus very high. Sternum as wide as long, truncate between posterior coxae which are separated by their width. Legs short and stout, fourth longest, others subequal, first sometimes shortest. A comb present on fourth tarsus. Integument of abdomen appearing leathery and folded with small sclerotized plates and many small sclerotized spots, the bases of hairs. Spinnerets framed by a sclerotized ring. Colulus not visible. Abdomen overhanging carapace except for eye region.

The genitalia of only three species, *O. trituberculata* (Hickman) of Tasmania, of *O. paradoxa* (Lucas) and *O. americana* (Emerton) were examined. On first appearance the palpus of the Tasmanian species seems different. The embolus of this species, though similar in shape to that of *O. paradoxa* and other theridiids close to *Theridion*, is quite small and partially hidden by a portion of the large radix. The median apophysis (M in figs. 1 and 4) of all species examined has lost its function of holding the bulb in the cybium (Y). The median apophysis appears nonfunctional in *O. trituberculata* and *O. paradoxa*, and has moved to a more mesal and ventral position. In *O. americana* this structure supports the embolus (E). The tubercle in the alveolus of the cymbium (Y) has moved to the ectal margin of the cymbium and has become a hook-shaped structure which might be called the paracymbial hook. The conductor (C) is a small extension of the tegulum and may have a translucent tip. The radix (R) may be quite complex and supports the tip of the embolus (E). The subtegulum (S) is very shallow. The epigynum consists of a strongly sclerotized plate. The ducts open into a depression or into minute openings in this plate.

Oronota americana has been collected by sweeping shrubs, (Kaston, 1948). Only recently did Prof. Bonnet (1952) rediscover the name *Oronota*, which has precedence over the better known *Ulesanis*.

Ulesanis serrata Emerton, 1913, Trans. Connecticut Acad. Sci. 18: 213, pl. 1, fig. 5, ♂ does not belong in this genus. It is a synonym of *Paidisca marxi* (Crosby), 1906.

Oronota paradoxa (Lucas)

Figure 9

Epeira paradoxa Lucas, 1846, Exploration scient. de l'Algérie. Zool. 1. Arachn. p. 251, pl. 15, fig. 7, ♀.

This species is found in southern Europe. The illustration (fig. 1) was made from a cotype. The epigynum of the female is much like that of *O. americana*, although the openings are easier to see.

Oronota americana (Emerton), new combination

Figures 1–8

Ulesanis americana Emerton, 1882, Trans. Connecticut Acad. Sci. 6: 28, pl. 6, fig. 1, ♂, ♀. Keyserling, 1886, Die Spinnen Amerikas, Theridiidae 2: 17, pl. 11, fig. 142, ♀. Marx, 1889, Proc. U. S. Nat. Mus. 12: 525. Marx, 1892, Proc. Ent. Soc. Washington 2: 156. Simon, 1894, Histoire Naturelle des Araignées 1: 557. Banks, 1895, Jour. New York Ent. Soc. 3: 85. Banks, 1904, Proc. Acad. Nat. Sci. Philadelphia:, 56: 127. Bryant, 1908, Occas. Pap. Boston Soc. Nat. Hist. 7: 15. Banks, 1910, Bull. U. S. Nat. Mus. 72: 23. Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist. 29: 213. Comstock, 1912, The Spider Book, p. 356, fig. 359, ♂, ♀. Barrows, 1918, Ohio Jour. Sci. 18:305. Bishop and Crosby, 1926. Jour. E. Mitchell Sci. Soc. 41: 184. Crosby and Bishop, 1928, Mem. Cornell Univ. Agric. Exp. Sta. 101: 1042. Kaston, 1938, Bull. Connecticut Geol. Nat. Hist. Surv. 60: 186. Bryant, 1940, Bull. Mus. Comp. Zool.

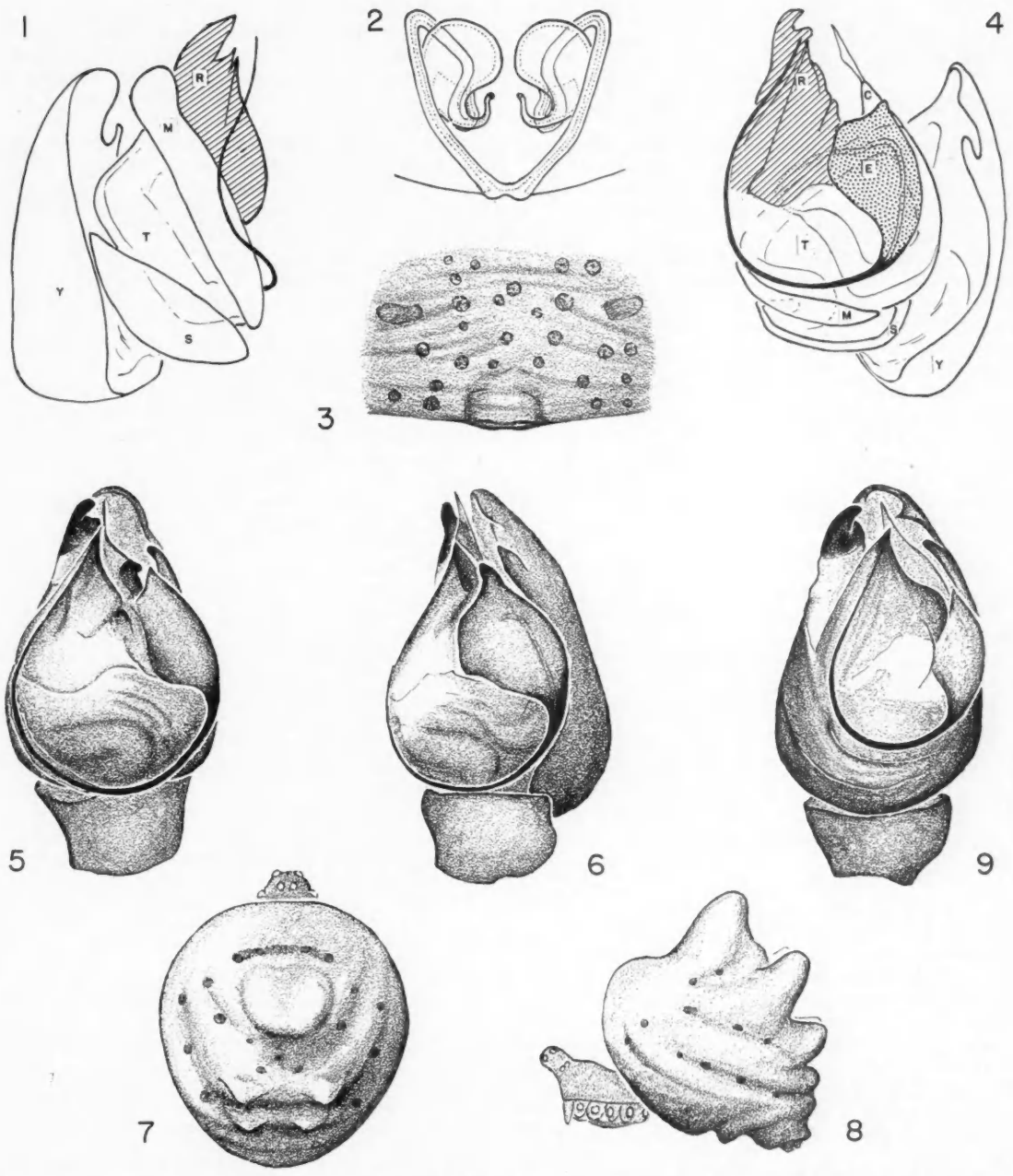

Fig. 1–8. *Oronota americana* (Emerton). FIG. 1. Left palpus, mesal view, expanded. FIG. 2. Female genitalia, dorsal view. FIG. 5. Epigynum. FIG. 4. Palpus, subventral view, expanded. FIG. 5. Palpus, ventral view. FIG. 6. Palpus, ectal view. FIG. 7. Female, dorsal view. FIG. 8. Female, lateral view.

FIG. 9. *Oronota paradoxa* (Lucas), palpus, ventral view, cotype.

(C, conductor; E, embolus; M, median apophysis; R, radix; S, subtegulum; T, tegulum; Y, cymbium.)

86: 302. Comstock, 1940, The Spider Book, rev. edit., p. 371, fig. 359, ♂, ♀. Roewer, 1942, Katalog der Araneae 1: 390. Chamberlin and Ivie, 1944, Bull. Univ. Utah Biol. Ser., 8: 57. Muma, 1945, Bull. Univ. Maryland Agric. Exp. Sta. A38: 30. Archer, 1946, Pap. Alabama Mus. Nat. Hist., 22: 57. Kaston, 1948, Bull. Connecticut Geol. Nat. Hist. Surv. 70: 96, fig. 112–119, ♂, ♀. Lowrie, 1948, Ecology 29: 338.

Male: Cephalothorax, legs and sclerotized portions of the abdomen usually reddish brown. Abdomen except for sclerotized portions, white with irregular dusky to black spots which vary in different individuals.

Carapace pear-shaped, drawn out above clypeus into a lobe on which eyes are located. Anterior eye row procurved, posterior recurved. Anterior median eyes separated by about three-quarters of their diameter, one and one-quarter diameter from laterals. Posterior median eyes separated by one diameter, by one and one-half diameter from laterals. Anterior median eyes slightly larger (ratio 1: 0.8) than others. Height of clypeus equals about four and one-half diameters of anterior median eyes. Sternum granulated, pointed between coxae, with two slight lobes, separated by a furrow between fourth coxae which are separated by their length. Fourth coxae with a tubercle pointing towards sternum, other coxae with a slight indication of this. Fourth legs longest, others subequal. Slight tubercles on retrolateral surface of patellae. Abdomen with a median hump and several paired protrusions which are less distinct in the male than in the female (figs. 7, 8). Epigastric plates sclerotized. Palpus illustrated by figures 1, 4–6.

Total length of males 1.3–1.6 mm. Measurements of a specimen from Connecticut: total length, 1.5; carapace, 0.69 long, 0.71 wide, 0.55 high; first patella and tibia, 0.52; second patella and tibia, 0.51; third patella and tibia, 0.41; fourth femur, 0.60, patella and tibia, 0.59, metatarsus, 0.26, tarsus, 0.27.

Female: Coloration and structure like that of male, but cephalic lobe smaller. There is considerable variation in color, the spacing of the eyes and the shape of the abdomen (figs. 7 and 8). Only the larger sclerotized spots are shown on the illustrations, the innumerable small circular spots (from which project small hairs) are not shown. The epigynum (fig. 3) as well as the internal genitalia, (fig. 2) differ in degree of sclerotization in different individuals. The female of *O. americana* differs from *O. paradoxa* of Europe in that the openings in the epigynum of the former are minute, while the openings of a *paradoxa* are very small slits.

Total length of females, 1.7–2.7 mm. Measurements of a female from New Jersey: total length, 2.2; carapace, 0.80 long, 0.78 wide, 0.52 high; first, second and third patellae and tibiae 0.52; fourth femur, 0.65, patella and tibia, 0.69, metatarsus, 0.33, tarsus, 0.35.

TYPE SPECIMENS: Cotypes from Beverly and Danvers, Massachusetts and New Haven, Connecticut, swept from bushes, in the Museum of Comparative Zoology.

RECORDS: *Massachusetts:* Essex County: Peabody (Bryant, 1908). Norfolk County: Milton (Bryant, 1908). *Connecticut:* Hartford County: Hazardville (H. L. Johnson). New Haven Co: South Meriden (H. L. Johnson); New Haven (Kaston, 1948). Fairfield County: Rowayton (C. J. Goodnight). *New York:* Erie County: Marilla (Crosby and Bishop, 1928). Tompkins County: Ithaca (Crosby and Bishop, 1928). Onondaga County: Jamesville (Crosby and Bishop, 1928). Ulster County: Mount Marion (Crosby and Bishop, 1928). Suffolk County: Riverhead (Crosby and Bishop, 1928). *New Jersey:* Bergen County: Ramsey (W. J. Gersch). *Ohio:* Hocking County: Rockbridge (Barrows, 1918). *Michigan:* Berrien County: Warren's Woods (Lowrie, 1948). *Indiana:* Porter County: Dunes State Park (H. S. Dybas). *Maryland:* Prince Georges County (Muma, 1945). *District of Columbia:* (Marx, 1892). *North Carolina:* Watauga County: Blowing Rock (Bishop and Crosby, 1926) *Tennessee:* Wilson County: Cedars of Lebanon State Park (Archer, 1946). *Mississippi:* Wilkinson County: Centreville (A. F. Archer). *Alabama:* Lawrence County: Wheeler Dam (A. F. Archer). Jefferson County: Shade's Mountain (Archer, 1946). Tuscaloosa County: Rock Mountain (Archer, 1946); Hurricane Creek (Archer, 1946). Monroe County: Claiborne (Archer, 1946); Randon's Creek (Archer, 1946). Dale County: south of Ariton (Archer, 1946). Escambia County: Little River State Park (Archer, 1946). Mobile County: Cedar Creek State Park (Archer, 1946); Spring Hill (Archer, 1946). Baldwin County: Gasque (A. F. Archer); Dyas Creek (Archer, 1946); Hog Creek (Archer, 1946). *Georgia:* Screven County: east of Sylvania (Chamberlin and Ivie, 1944). Ware County: Waycross (W. J. Gertsch). *Florida:* Jackson County: 8 mi. nw. of Marianna

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EXPLANATION OF PLATE II

FIG. 10. *Stemmops cambridgei* n. sp., male, carapace, lateral view.

FIG. 11. *Stemmops victoria* n. sp., female, abdomen, dorsal view.

FIG. 12–13. *Stemmops lina* n. sp. FIG. 12, Male, carapace, dorsal view. FIG. 13. Male, carapace, lateral view.

FIG. 14. *Stemmops bicolor* O. P.-Cambridge, female, dorsal view.

FIG. 15. *Stemmops lina* n. sp., female, dorsal view.

FIG. 16. *Stemmops ornata* (Bryant), female, dorsal view.

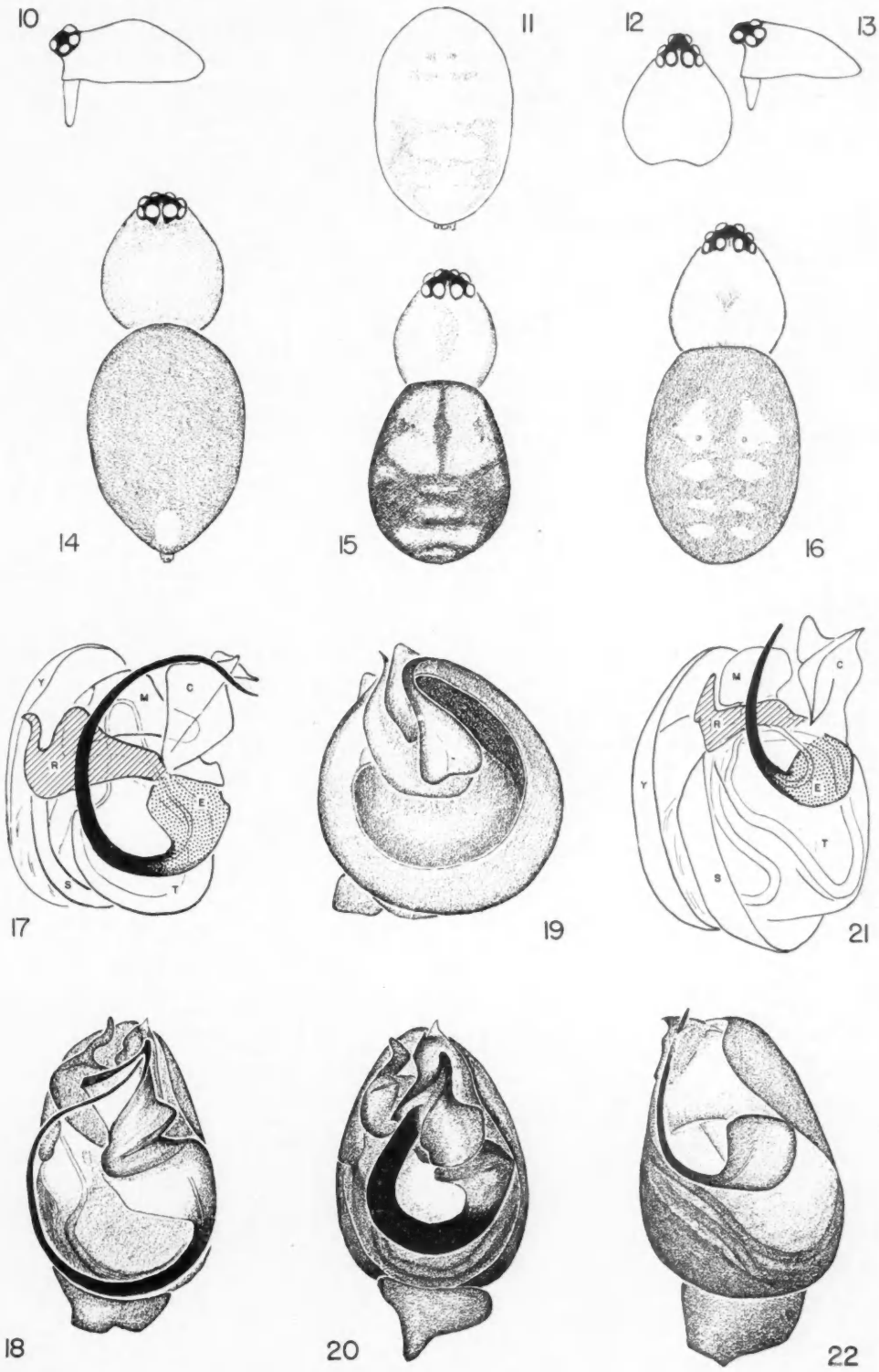
FIG. 17–18. *Stemmops bicolor* O. P.-Cambridge. FIG. 17, Left palpus, subventral view, expanded. FIG. 18. Palpus, ventral view.

FIG. 19. *Stemmops lina* n. sp., palpus, ventral view.

FIG. 20. *Stemmops cambridgei* n. sp., palpus, ventral view.

FIG. 21–22. *Stemmops ornata* (Bryant). FIG. 21. Palpus, subventral view, expanded. FIG. 22, Palpus, ventral view.

(C, conductor; E, embolus; M, median apophysis; R, radix; S, subtegulum; T, tegulum; Y, cymbium.)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(Archer, 1946). Highlands County: Lake Ishtopaka (A. M. Nadler); Lake Placid (A. M. Nadler). Sarasota County: Sarasota (A. M. Nadler). Martin County: Indian Town (W. J. Gertsch). Monroe County: Tavernier (A. M. Nadler). Dade County: n. of Homestead. *Cuba:* Pico Turquino (Bryant, 1940).

Stemmops O. P.-Cambridge

Stemmops O. P.-Cambridge, 1894, Biologia Centrali Americana, Araneidea 1: 125. Genotype: *Stemmops bicolor* O. P.-Cambridge.

Ataulfo O. P.-Cambridge, 1896, Biologia Centrali Americana, Araneidea 1: 178. Genotype: *Ataulfo nugax* O. P.-Cambridge (= *S. bicolor* O. P.-Cambridge).

Mettus O. P.-Cambridge, 1899, Biologia Centrali Americana, Araneidea 1: 292. Genotype: *Mettus reclivis* O. P.-Cambridge (= *S. bicolor* O. P.-Cambridge).

Small theridiid spiders with carapace nearly circular in outline, usually highest in thoracic region (fig. 10). Eye region slightly elevated, black in color and eyes very large and usually separated by less than their diameter. Laterals and frequently anterior and posterior medians subcontiguous with laterals. Anterior eye row, as seen from in front straight or procurved, posterior row seen from above, straight to recurved. Ocular quadrangle slightly longer than wide, frequently much narrower in front than behind. Eyes subequal or anterior medians smaller than others. Clypeus concave. Sternum as long as wide, truncate between posterior coxae which are separated by their diameter. Legs fairly short, fourth longer than first, third shortest. Fourth tarsi with small and indistinct comb. Abdomen oval, two setae on small colulus usually visible. Carapace of male *S. lina* n. sp. slightly modified by being pointed between anterior median eyes, with eye region projecting over clypeus (fig. 12, 13).

Epigynum a simple pit of indistinct outline. The connecting ducts open into the side of the pit. Walls of ducts sclerotized, making lumen difficult to discern. One pair of seminal receptacles present. Palpus with tip of embolus (E in fig. 17, 21) usually shaped as in theridiids allied to *Theridion*. Tip of embolus supported by conductor (C) which is a complex sclerite. Median apophysis (M) a separate sclerite lying, as usual, in a pocket of the alveolus of the cymbium (Y) holding upper portion of the bulb in the cymbium. Radix (R) present with no apparent function. Duct in some species looping through the median apophysis. *S. lina* has the conductor supporting the whole length of the thread-shaped embolus. The relatively large eyes grouped closely together, the sclerotized internal female genitalia, the conductor that supports the embolus, and the shape and position of the median apophysis differentiate this genus from others.

Gertsch (1949) reports that *Stemmops* does not spin a web but hunts its prey. Members of this genus are known from the region under consideration here.

Stemmops concolor Simon, 1897, Proc. Zool. Soc. London, p. 861, described from St. Vincent Island, Lesser Antilles, is not known to me.

Stemmops bicolor O. P.-Cambridge

Figures 14, 17, 18, 35, 36

Stemmops bicolor O. P.-Cambridge, 1894, Biologia Centrali Americana, Araneidea, 1: 125, pl. 17, fig. 5, ♂. Simon, 1897, Histoire Naturelle des Araignées 2:989. F. O. P.-Cambridge, 1902, Biologia Centralia Americana, Araneidea 2: 400. Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist. 29: 188. Roewer, 1942, Katalog der Araneae 1: 459. Chamberlain and Ivie, 1944, Bull. Univ. Utah, Biol. Ser. 8: 46. Archer, 1946, Pap. Alabama Mus. Nat. Hist. 22: 55.

Ataulfo nugax O. P.-Cambridge, 1896, Biologia Centrali Americana, Araneidea 1: 178, pl. 22, fig. 7, ♂.

Mettus reclivis O. P.-Cambridge, 1899, Biologia Centrali Americana, Araneidea 1: 293, pl. 38, fig. 8, ♀.

Stemmops darlingtoni Bryant, 1940, Bull. Mus. Comp. Zool. 86: 316, fig. 87, 89, ♀.

Male: Carapace yellow, eye region black, some duskiness on sides and in cephalic region. Sternum, legs yellow. Abdomen grey to black with a white spot above spinnerets (figs. 14), venter lighter.

Both eye rows straight. Anterior median eyes separated by about one-quarter their diameter, other eyes by about the same distance or slightly less. Anterior median eyes smallest, lateral eyes 1.3, posterior median eyes 1.4 diameter of anterior medians. Height of clypeus about two and one-half diameters of anterior median eyes. Palpus illustrated by figures 17 and 18.

Total length of males 1.7–2.0 mm. Measurements of a male from Tamaulipas; total length, 1.7; carapace, 0.81 long, 0.79 wide, 0.45 high; first patella and tibia, 1.17; second patella and tibia, 0.76; third patella and tibia, 0.85; fourth femur, 0.91 patella and tibia, 1.24, metatarsus, 0.65, tarsus, 0.50.

Female: Coloration and general appearance like that of male although the carapace is lower. Anterior median eyes one-quarter of their diameter apart, others almost touching. Eye sizes as in male. Height of clypeus one and three-quarters diameter of anterior median

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EXPLANATION OF PLATE III

FIG. 23–24. *Stemmops crypta* n. sp., FIG. 23. Female genitalia, cleared, ventral view. FIG. 24. Epigynum.

FIG. 25–26. *Stemmops lina* n. sp. FIG. 25. Female genitalia, dorsal view, FIG. 26. Epigynum.

FIG. 27–28. *Stemmops victoria* n. sp. FIG. 27. Female genitalia, ventral view, cleared. FIG. 28. Epigynum.

FIG. 29–30. *Stemmops ornata* (Bryant). FIG. 29. Female genitalia, dorsal view. FIG. 30. Epigynum.

FIG. 31–32. *Stemmops cambridgei* n. sp. FIG. 31. Female genitalia, dorsal view. FIG. 32. Epigynum.

FIG. 33–34. *Stemmops questa* n. sp. FIG. 33. Female genitalia, dorsal view. FIG. 34. Epigynum.

FIG. 35–36. *Stemmops bicolor* O. P.-Cambridge. FIG. 35. Female genitalia, dorsal view. FIG. 36. Epigynum.

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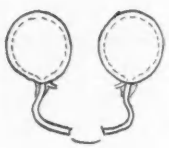

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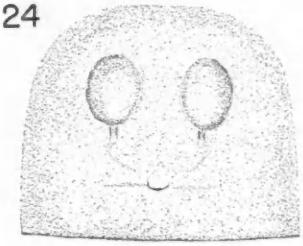

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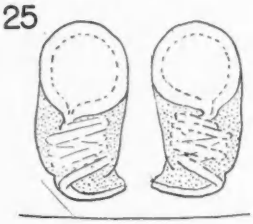

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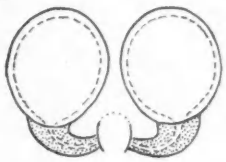

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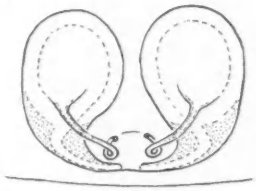

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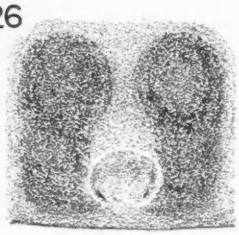

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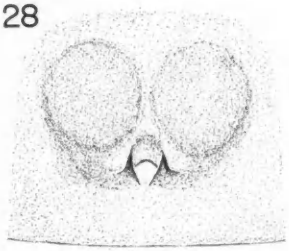

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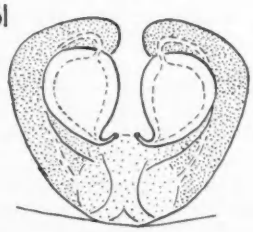

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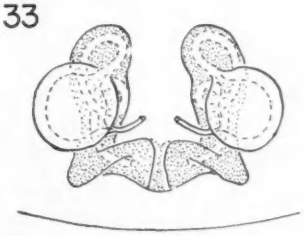

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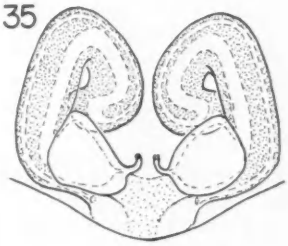

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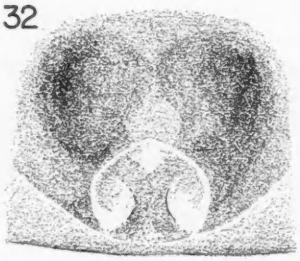

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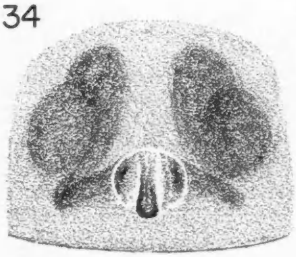

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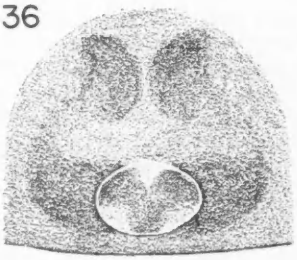

eyes. Epigynum with a three forked sclerotized piece visible in the depression which apparently supports the seminal receptacles. Connecting ducts make a large loop (fig. 35, 36).

Total length of females 1.6–2.1 mm. Measurements of a female from Oaxaca: total length 2.0; carapace, 0.75 long, 0.68 wide, 0.26 high; first patella and tibia, 1.04; second patella and tibia, 0.75; third patella and tibia, 0.67; fourth femur, 0.90, patella and tibia, 1.14, metatarsus, 0.58, tarsus, 0.50.

The color of the carapace in some individuals is much darker, being almost brown. There are slight differences in the eye size and also in the shape of the thumb of the radix and the conductor of the palpus.

TYPE LOCALITY: The holotypes of *S. bicolor*, *Ataulfo nugax* and *Mettus reclivis* came from Teapa in Tabasco, Mexico (H. H. Smith). F. O. P.-Cambridge reported the types to be in the collection of Godman and Salvin. The female holotype and two female paratypes of *S. darlingtoni* were collected in Soledad, Cuba, August 1934 by P. J. Darlington and are in the collection of the Museum of Comparative Zoology.

RECORDS: *Georgia:* Screven County: north of Sylvania, April 15, 1943, ♀ (W. Ivie). *Florida:* "Mineral City", Feb. 20, 1936, ♂, ♀ (S. C. Bishop). Lee County: Fort Myers, Jan. 20, 1939, ♂, ♀. Highlands County: Lake Placid, Feb. 1943, 2 ♀ (M. Cazier). Orange County: Winter Park, March, 1939, ♀ (F. E. Lutz). Hillsborough County: Tampa, Aug. 26, 1933. 4 ♀ (W. Ivie). Alachua County: Micanopy, March 6, 1927, ♀ (J. Leonard); nr. Newnan's Lake, June 13, 1935, ♀ (W. Ivie); March 19, 1938, ♀, juv. (W. J. Gertsch). *Alabama:* Clarke County: Thomasville, Feb. 1941, juv. (Archer, 1946). *Mississippi:* Wilkinson County: Centreville, April, 1944, ♀ (Archer, 1946). *Texas:* Starr County: 5 mi. e. of Rio Grande City, May 1, 1937, ♂ (S. Mulaik). Hidalgo County: 5 mi. s. of San Juan, Feb. 22, 1935, 2 ♀ (S. Mulaik). Cameron County: Jan. 1936, ♂ (L. I. Davis); Oct. 1936, ♂ (L. I. Davis). Big Tree Vine Association, Sept. 1936, ♂, 2 ♀, 4 juv. (L. I. Davis). *Nuevo Leon:* 6 mi. n. of Linares, July 3, 1936, 2 ♀ (L. I. Davis); Cañon de Las Anahuas, near Linares, July 18, 1942, ♂, 5 ♀, 5 juv. (F. Bonet and D. Pelaez). *Tamaulipas:* Río Frio, near Ciudad Mante, Dec. 25, 1939, 2 ♂ (F. Norman). *San Louis Potosí:* Tamazunchale, July 8, 1944, 2 ♀ (L. I. Davis); April 15, 1946, ♀ (L. I. Davis and M. Johnston). *Veracruz:* June 22, 1936, ♀ (L. I. Davis); Veracruz, July 1, 1953, ♀ (C. and M. Goodnight); La Buena Ventura, July, 1909, 4 ♀; La Planta de Moctezuma, near Fortin, July 7, 1947, ♀ (C. and M. Goodnight). *Oaxaca:* Tolosa, n. of Palomares, Sept. 1–12, 1947, ♀ (B. Malkin); Aug. 23–30, 1947, ♀ (B. Malkin). *Costa Rica:* San José, ♀ (E. Schmidt). *Bahama Islands:* South Bimini, May, 1951, ♂, 16 ♀ (W. J. Gertsch and M. A. Cazier); June, 1951, ♂ (M. A. Cazier, C. and P. Vaurie).

Stemmops cambridgei, new species

Figures 10, 20, 31, 32

Male: Coloration like that of *S. bicolor*. Carapace typical (fig. 10). Anterior eye row slightly procurved, posterior row straight. Anterior median eyes separated by slightly less than one-quarter of their diameter. Other eyes almost touching. Size of posterior median eyes, 1.3 diameter, laterals 1.2 diameter of anterior median eyes. Height of clypeus two and one-half diameters of anterior median eyes. Palpus with a very short wide embolus which differentiates this from other species of *Stemmops* (fig. 20).

Total length of males, 1.4–1.7 mm. Measurements of holotype; total length 1.7; carapace 0.75 long, 0.75 wide; first patella and tibia,1.30; second patella tibia, 0.80; third patella and tibia, 0.78; fourth femur 0.95, patella and tibia, 1.24, metatarsus, 0.66, tarsus, 0.55.

Female: Coloration and structure like that of male except for eyes being slightly farther apart. Anterior median eyes separated by one-quarter diameter, one-eighth their diameter from laterals. Posterior median eyes separated by one-eighth their diameter and by the same distance from laterals. Clypeus two diameters of anterior median eyes. The depression of the epigynum is larger than in *S. bicolor*. The sclerotization of the internal genitalia is so heavy that the lumen of the connecting ducts could not be completely seen (fig. 31, 32).

Measurements female allotype; total length 1.7 mm.; carapace 0.69 long, 0.68 wide; first patella and tibia, 1.04; second patella and tibia, 0.74; third patella and tibia, 0.74; fourth femur, 0.92, patella and tibia, 1.17, metatarsus, 0.60, tarsus, 0.52.

TYPE LOCALITY: Male holotype and female allotype from Chiapas, between San Antonio and El Real, July 9, 1950 (C. and M. Goodnight and L. Stannard).

RECORDS: *Chiapas:* Finca Cuauhtemoc, near Cacahoatán, Aug. 7, 1950, ♂ paratype (C. Goodnight). *Tabasco:* Baños de Sulfre, near Teapa, Aug. 1, 1948, 2 ♂ paratypes (C. and M. Goodnight); Teapa, July 17, 1947 ♂ paratype (C. and M. Goodnight). *Yucatan:* Chichen Itza, July 10, 1948, 2 ♂ paratypes (C. and M. Goodnight); June 25, 1951, 5♂, 8 ♀, 3 juv. paratypes (L. Stannard). *Honduras:* La Ceiba, ♀ paratype (F. J. Dyer).

The genitalia (figs. 10, 31, 32) will serve to distinguish this from other known species of the genus.

Stemmops questa, new species

Figures 33, 34

Female: Coloration differs from that of the preceding two species in that carapace, sternum

and legs are more orange in color and in that the venter of the abdomen is white.

The carapace is slightly longer than wide. Anterior median eyes separated by two-thirds their diameter, almost touching laterals. Posterior median eyes one-sixth diameter apart and almost touching laterals. Posterior median eyes almost twice the diameter of anterior medians, laterals 1.8 diameter of anterior medians. Height of clypeus two diameters of anterior median eyes. Epigynum appears almost to have a septum. The lumen of the connecting ducts differs from that of other species in having loops but these are difficult to see because of the heavy sclerotization of its walls (fig. 33, 34).

Measurements of female holotype: total length 1.6 mm.; carapace, 0.66 long, 0.60 wide; first patella and tibia, 0.81; second patella and tibia, 0.62; third patella and tibia, 0.56; fourth femur, 0.71, patella and tibia, 0.92, metatarsus, 0.45, tarsus, 0.44.

TYPE LOCALITY: Female holotype from Finca Cuauhtemoc, near Cacahoatán, Chiapas, 4–5000 feet elevation, August 12, 1950, (C. and M. Goodnight).

The genitalia (figs. 33, 34) will serve to distinguish this from other known species of the genus.

Stemmops ornata (Bryant)

Figures 16, 21, 22, 29, 30

Euryopis ornata Bryant, 1933, Bull. Mus. Comp. Zool. 74: 172, fig. 2, 3 ♂. Roewer, 1942, Katalog der Araneae 1: 454.

Euryopis orniceps Chamberlain and Ivie, 1944, Bull. Univ. Utah, Biol. Ser. 8: 43, fig. 86, 123, ♂.

Male: Coloration quite variable. Carapace light yellow sometimes with a central dusky spot, eye region black as usual. Sternum, legs, light yellow. Abdomen grey with a series of white spots (fig. 16), venter lighter grey to white.

Carapace longer than wide, highest near posterior eye row, eyes relatively small and far apart compared to other members of this genus. Anterior eye row straight, posterior row recurved. Ocular quadrangle slightly longer than wide. Anterior median eyes separated by slightly less than one diameter; almost touching laterals. Posterior medians separated by two-thirds their diameter and by one-third from laterals. Eyes subequal in size. Height of clypeus about two and one-quarter diameters of anterior median eyes. Sternum almost circular. In contracted palpus, embolus appears as a prominent ventral sclerite (fig. 22). If expanded, the palpal parts are in the same position as in other species of *Stemmops* (fig. 21). The shape of the embolus varies slightly in different individuals.

Total length of males: 1.3–1.7 mm. Measurements of a male from Ohio: total length, 1.6; carapace, 0.65 long, 0.55 wide; first patella and tibia, 0.80; second patella and tibia, 0.61; third patella and tibia, 0.59; fourth femur, 0.66, patella and tibia, 0.91, metatarsus, 0.36, tarsus, 0.47.

Female: Coloration and structure except for eyes like that of male. Ocular quadrangle as long as wide behind, slightly narrower in front. Anterior median eyes three-quarters of their diameter, apart, almost touching laterals. Posterior median eyes separated by one-third their diameter by one-sixth from laterals. Posterior median eyes 1.2, lateral eyes 1.1 diameter of anterior median eyes. Height of clypeus one and three-quarters diameters of anterior median eyes. Epigynum a very small depression with anterior lip. Internal genitalia sclerotized (figs. 29, 30).

Total length of females 1.8–1.9 mm. Measurements of a female from Ohio; total length, 1.9; carapace, 0.77 long, 0.65 wide; first patella and tibia, 0.77; second patella and tibia, 0.65; third patella and tibia, 0.58; fourth femur, 0.71, patella and tibia, 1.00, metatarsus, 0.39, tarsus, 0.47.

TYPE LOCALITIES: The male holotype of *Euryopis ornata* come from Meridian, Lauderdale County, Mississippi (H. E. Weed) and is in the Museum of Comparative Zoology. The male holotype of *Euryopis orniceps* came from south east of Toccoa, Stephens County, Georgia, April 29, 1943 (W. Ivie) and is in the collection of the University of Utah.

RECORDS: *New Jersey:* Hunterdon County: Lambertville, May 19, 1953, ♂ ♀ (W. Ivie). *Ohio:* Hocking County: June 5, 1938, ♂ ♀. *North Carolina:* Polk County: Tryon, Nov. 21, 1949, ♀ in leaf mold (L. Eisenach and O. Park); Wake County: Raleigh, Nov. 8, 1937, ♂ (C. S. Brimley and D. L. Wray). *Georgia:* Rabun County: between Clayton and Tallulah Falls, April 28, 1943, ♂ (Chamberlin and Ivie, 1944). *Mississippi:* Tishomingo County: Tishomingo State Park, Sept. 5, 1941, juv. (C. and M. Goodnight).

Stemmops victoria, new species

Figures 11, 27, 28.

Color all yellowish white except for the black eye region and some very light dusky patches on the dorsum of the abdomen (fig. 11).

Structure of carapace typical. Anterior median eyes separated by their diameter, almost touching laterals, posterior median eyes one-third of their diameter apart, almost touching laterals. Posterior median and all lateral eyes 1.8 diameter of anterior medians in size. Height of clypeus equals about two diameters of anterior median eyes. Epigynum and internal female genitalia (fig. 27, 28) differ only in detail from *S. ornata*.

Measurements of female holotype; total length 1.3 mm.; carapace 0.52 long, 0.47 wide; first patella and tibia, 0.61; second patella and tibia, 0.41; third patella and tibia, 0.40; fourth femur, 0.48,

patella and tibia, 0.73, metatarsus, 0.26, tarsus, 0.31.

TYPE LOCALITY: Female holotype from Ciudad Victoria, Tamaulipas July 2, (A. M. and L. I. Davis).

The genitalia (figs. 27, 28) will serve to distinguish this from other known species of the genus.

Stemmops crypta, new species

Figures 23, 24

Female: Carapace dusky, darker along margins. Legs yellow white. Abdomen light grey, with a white patch above spinnerets.

Carapace appearing wide, about 1.4 times width of posterior eye row at this level. Anterior median eyes separated by one diameter, touching laterals. Posterior median eyes separated by one and three-quarters diameters and touching laterals. Anterior lateral eyes and posterior eyes about 1.7 diameter of anterior medians. Height of clypeus equals two and one-half diameters of anterior median eyes. Epigynum (fig. 24) a very indistinct line, the posterior border of a depression. Seminal receptacles, which are visible without clearing, separated by their diameter from each other and by their length from the opening (figs. 23, 24).

Measurements of female holotype, total length, 1.3 mm.; carapace 0.55 long, 0.50 wide; first patella and tibia, 0.74; second patella and tibia, 0.55; third patella and tibia, 0.48; fourth femur, 0.65, patella and tibia, 0.75, metatarsus, 0.43, tarsus, 0.33.

TYPE LOCALITY: Female holotype from Barro Colorado Island, Canal Zone, July 21, 1938.

The genitalia (figs. 23, 24) will serve to distinguish this from other known species of the genus.

Stemmops lina, new species

Figures 12, 13, 15, 19, 25, 26

Male: Carapace orange yellow, dusky around sides, dusky in cephalic region, eye area black. Sternum yellow, dusky around sides. Legs yellow to brown, with some dusky patches or stripes on pro- and retro-lateral surfaces of femora, patellae and tibiae. Abdomen light grey with a black pattern on dorsum and five white spots, four of these near the center and one above spinnerets (fig. 15). Sides of abdomen black, venter light grey with a transverse black band just anterior to spinnerets.

Structure of carapace slightly modified, highest in eye region, and with a narrow pointed extension between the anterior eyes, hanging over the clypeus (fig. 12, 13). Anterior eye row strongly procurved, posterior row slightly recurved. Anterior median eyes separated by two-thirds their diameter, almost touching laterals. Posterior medians separated by one-third their diameter, almost touching laterals. Posterior medians and all lateral eyes 1.6 diameter of anterior medians. Height of clypeus equals about three diameters of anterior median eyes. First and fourth legs almost equal in length. Superficially, palpus (fig. 19) quite distinct; however when expanded, structure like that of other species. Embolus a fine thread, the whole length of which is supported by a huge extension of a lobe of the conductor; tip of embolus, as in other species of *Stemmops*, lying on the main portion of the conductor; both the tip of the embolus and a portion of the conductor lying in a fold of the cymbium; radix medium-sized.

Measurements of male holotype: total length, 1.0 mm.; carapace, 0.44 long, 0.41 wide; first patella and tibia, 0.53; second patella and tibia, 0.41; third patella and tibia, 0.39; fourth femur, 0.41, patella and tibia, 0.60, metatarsus, 0.21, tarsus, 0.24.

Female: Coloration like that of male. Structure of carapace typical for genus. Anterior eye row procurved, posterior row straight. Anterior median eyes separated by three-quarters their diameter, almost touching laterals. Posterior median eyes separated by one-third their diameter, almost touching laterals. Posterior median eyes and all lateral eyes 1.8 diameter of anterior median eyes. Height of clypeus equal to about three diameters of anterior median eyes. First and fourth legs subequal, second and third legs subequal. Epigynum an indistinct depression with an opening on each side (fig. 26). The lumen of the connecting ducts coiled and difficult to discern (fig. 25).

Total length of females 1.1–1.2 mm. Measurements of the female allotype: total length, 1.2; carapace, 0.52 long, 0.45 wide; first patella and tibia, 0.52; second patella and tibia, 0.39; third patella and tibia, 0.39; fourth femur, 0.45, patella and tibia, 0.62, metatarsus, 0.21, tarsus, 0.26.

TYPE LOCALITY: Male holotype, female allotype and one juvenile female paratype from Palenque Ruins in Chiapas, July 16, 1949, in soil (C. Goodnight).

RECORDS: *Puebla:* Maria Andreas near Huachinango, Aug. 24, 1946, ♀ paratype (C. Goodnight and E. Bordas). *San Luis Potosí:* Tamazunchale, May 20, 1944, ♀ paratype (F. Bonet).

The genitalia (figs. 25, 26) will serve to distinguish this from other known species of the genus.

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INFLUENCE OF SUGARS ON OVIPOSITION OF NARCISSUS BULB FLY

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The normal food of narcissus bulb fly (*Lampetia equestris* (F.)) adults is commonly believed to be nectar or pollen. Adults have been observed visiting the flowers of plants, such as dandelion and wild buttercup, that are prevalent during the time they are most abundant. Studies were made to determine whether the nectar or the pollen was the objective of these visits. The authors observed that the flies were feeding on the nectar rather than on the pollen. To determine the influence of the food on oviposition, cage tests were conducted under greenhouse conditions. Adults were reared in the greenhouse slightly in advance of the season of normal occurrence outdoors.

Single pairs of flies were caged in lantern-globe cages placed over potted narcissus plants (Fig. 1). The tops of the lantern globes were fitted with a coarse netting. A small vial with cotton wick was attached to a stake close to each plant to furnish food or water.

In the first experiment diluted honey was used as food and compared with water alone. In some of the cages pollen was made available by placing a dandelion flower on the netting at the top of the cage. The cages were examined and the eggs removed daily. If a female died, a new one was placed in the cage, or a new pair if the male was dead also. Males were not replaced if mating had been observed. Eggs were usually laid in the loose soil near the base of the plant, but occasionally some were found stuck to the leaves. The length of life of the females and the numbers of eggs deposited are given in table I.

TABLE I

LENGTH OF LIFE AND NUMBERS OF EGGS LAID BY NARCISSUS BULB FLIES FED VARIOUS COMBINATIONS OF HONEY, POLLEN, AND WATER

FOOD	NUMBER OF FEMALES	AVERAGE DAYS ALIVE	AVERAGE NUMBER OF EGGS LAID
Diluted honey	12	16.2	76.1
Diluted honey and pollen	13	16.7	83.4
Water and pollen	24	8.3	10.2
Water only	26	7.5	7.6

It is evident that the use of honey as food resulted in a much longer life and strongly influenced egg deposition. Nine flies, all among those receiving honey, laid more than 100 eggs each, the maximum being 174. Only three of the flies receiving honey failed to lay eggs, whereas 27 of the 50 that did not have honey laid no eggs.

FIG. 1. Lantern-globe cage used for egg-laying studies on the narcissus bulb fly.

Since it appeared that honey or some similar material was necessary as a food for the bulb flies, several types of sugars—maltose, dextrose, levulose, and sucrose—of high chemical purity were tested in comparison with honey. Eleven

[1]Resigned April, 1945.

TABLE II

NUMBERS OF EGGS LAID BY NARCISSUS BULB FLIES FED VARIOUS SUGARS

REPLICATE	HONEY	MALTOSE	DEXTROSE	LEVULOSE	SUCROSE	SUCROSE AND POLLEN	WATER AND POLLEN
1	44	39	150	73	1	119	0
2	94	72	117	103	119	127	0
3	76	56	1	127	135	159	0
4	111	0	0	144	78	53	50
5	3	31	65	60	135	108	0
6	86	12	97	79	19	144	0
7	68	37	123	42	27	101	0
8	14	29	20	36	54	101	39
9	0	30	0	33	49	0	1
10	0	63	49	27	56	96	0
11	23	61	0	35	68	71	0
Average.....	47	39	56	69	67	98	8

replicates were made, each replicate being started as sufficient pairs were available. One cage in each replicate was furnished sucrose with pollen available from dandelion flowers, and a check cage was supplied with water only in the feeding vial but with pollen also available. The sugars were in solution, and the honey was diluted with 4 parts of water. The results are presented in table II.

All the sugars were much more suitable as food for the flies than the water and pollen. No one type of sugar was significantly better than any of the others, although maltose was slightly less effective. There was a decided increase in egg deposition where pollen was made available to flies furnished sucrose.

These tests indicate that the principal food of the adults is the nectar of the flowers, although pollen is also ingested. It is evident that no particular type of sugar is essential, but that any of those usually found in honey—dextrose, levulose, and sucrose—would be satisfactory. In later work where flies were caged for egg production, molasses and corn syrup seemed to be satisfactory in inducing egg deposition, but detailed data were not taken for these materials.

ON THE RESPIRATION OF AN AQUATIC AFRICAN BEETLE, POTAMODYTES TUBEROSUS HINTON[1]

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Potamodytes tuberosus Hinton is an elmid beetle that inhabits fast-flowing water, and the observations described in this paper were mostly made on specimens collected from a tributary of the River Densu, Gold Coast, British West Africa.

FIELD OBSERVATIONS

The adult beetles were very abundant near Asuboi on the River Densu, but during the latter part of the dry season the flow of water down this river fell below that apparently necessary for their survival. They were, however, readily found in other more permanent streams in the hills around Apapam and Begoro, and it seems, therefore, that members of the genus are widely distributed over this region of Gold Coast.

The adults congregated on rock surfaces that were exposed to fast-flowing water, but they rarely occurred more than an inch or two below the surface of the water. They appeared to feed on the microbiological slime that covered the submerged rock surfaces. When exposed to a more or less unidirectional flow of water the beetles clung to the rocks with their heads facing the oncoming water, and their well developed claws enabled them to maintain their position even under torrential conditions. If disturbed the adults released their hold on the substrate and allowed themselves to be swept away by the water. Their natural buoyancy, however, soon brought them to the surface where they

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took wing and generally returned to the place from which they had been disturbed. Sometimes the beetles re-entered the water by alighting alongside and gently sidling into it. Frequently, however, they appeared to fly straight into the rushing water. The significance of this behaviour was not understood since it appeared unlikely that they could regain a foothold on the rocks under such conditions. The frequency with which disturbed beetles alighted on anything light in colour suggested that the light reflected from broken water might play some part in guiding the beetles to suitable habitats.

At Asuboi the bed of the river was composed of large irregular rock slabs and boulders, and during the rainy season the flow of water was violent and torrential. Small parties of the beetles could then be found on many of the rocks that projected above the water level. They occupied a narrow zone at about water level, and were thus subjected to repeated short periods of immersion as a result of the rise and fall of the turbulent water. Under these conditions no specimens were seen to penetrate to a depth that would involve continuous immersion. During the dry season the flow of water steadily decreased, and the river became a series of basins and rock-pools connected by small channels and overflows. Although the rate of flow through the larger rock pools was extremely slow, faster currents, up to 125 cm. per second, were present in the connecting channels and overflows. The presence of such currents seemed to be essential for the survival of the adult beetles and they were never found in the slowly moving waters of the rock pools. In the section of the river which was most carefully observed, a stretch of some seventy yards, the beetles gradually became restricted to four places where the current was reasonably fast. As the dry season progressed and the flow down the river was further reduced, the beetles gradually deserted three of these four habitats, and, when living beetles were last seen at the fourth habitat, they numbered some 300 to 400 individuals. These were clustered in and around a small overflow about 9 inches long and four inches wide. Two days later all the beetles had disappeared from the fourth habitat, and no further specimens were seen in this stretch of the river during the remainder of the dry season. In suitable permanent streams the beetles may be found throughout the whole year.

All observations emphasized that the adults of *Potamodytes tuberosus* live only in running water. When such water becomes unavailable in a place previously inhabited by the beetles, they soon cease to remain there, even though apparently suitable food and quiet waters are still present.

THE RESPIRATORY BUBBLE

Adults of *Potamodytes* are readily detected in smooth running water since they carry a large silvery air bubble. Normally, the anterior edge of the bubble rests on the limbs and thorax of the beetle, but the posterior extremity is drawn out behind the beetle by the force of the current. The actual size and shape of the bubble depend on the force of the current and the position in which the beetle is standing, and bubbles have been observed to extend for 1½ inches. The presence of the bubbles suggested that the body contours of *P. tuberosus* were not streamlined to the same extent as are those of many insects that live exposed to strong currents.

In broken water containing an abundant supply of air bubbles, the respiratory bubble was maintained by the absorption of those bubbles which came into contact with it. Small bubbles were also detached from the posterior end of the respiratory bubble by the current so that the beetle was, in effect, living in a stream of air. Under these conditions the respiratory mechanism seemed to be quite obvious. On several occasions, however, the beetles were found in smoothly-flowing shallow water which was unbroken, and which apparently contained no obvious air bubbles. Such conditions were found, for instance, when the water from a large still pool flowed away over a smooth rock sill. Under such circumstances the beetles behaved quite normally, moving but little, and showing no signs of respiratory stress. Further, all the beetles in the same situation possessed bubbles of approximately the same size, an unlikely occurrence if the bubbles were of the well-known "shrinking air store" type (Ege, 1915). It seemed likely, in fact, that under these conditions the respiratory bubbles were acting as permanent physical gills, and the experimental work described below was carried out to ascertain the respiratory significance of the bubbles.

FACTORS INVOLVED IN MAINTAINING THE POSITION OF THE BUBBLE

Primarily the beetle retains the bubble because its body does not wet readily. Much of the body surface of adult *P. tuberosus* is covered with hydrophobe hairs and spines which increase the resistance of the surface to wetting. They are thus partly responsible for the presence of the bubble, but not for the form of the bubble, which is much deeper than the layer of hairs and stands entirely away from it.

Beetles, which had been out of the water for an hour or two, frequently "preened" themselves when returned to water. The abdomen would be extended so that the intersegmental membranes were exposed and the genitalia extruded, and the hind and middle legs were then rubbed against the sides and ventral surface of the abdomen. Finally, the forelegs were raised over and lowered behind the mid-legs, the fore- and mid-femora thus lying alongside each other. The femora were now rubbed vigorously together. It seemed probable that this behaviour was related to

some increased resistance of the beetle to wetting, though the mechanism was not at all clear. It is noteworthy, in this connection, that if any secretion had been produced by the intersegmental membranes of the abdomen, or by glands associated with the genitalia, then such behaviour would transfer the secretion to all the limbs. It was also observed that the elytra were frequently raised against the current of water, and the legs rubbed over the wings that were thus exposed. The wings and surfaces of the subelytral space were always very waxy and difficult to wet, and it seemed probable that rubbing the legs over the wings would transfer some of the waxy material onto the external surface of the beetle.

To sum up, most parts of the body do not wet readily as a result of the hydrophobe hairs present. In addition, the beetle may smear itself with oily or waxy substances that it secretes.

Fig. 1 shows that normal posture of the beetle and the position of the bubble when it is in a current of water. The tarsi and middle tibia always lie outside the bubble and wet readily. The only other parts of the insect to do so are the eyes. Presumably, vision would be impaired by a layer of air over the eyes as it would result in the distortion of light at the air water interface.

PROTECTION OF THE BUBBLE FROM THE PHYSICAL FORCE OF THE CURRENT

The lateral parts of the bubble lie behind, and are protected by, the rather flattened fore and middle femora. These are normally held so that the broad surfaces make an angle of approximately 45° with the current. The greater part of the bubble, however, lies over and behind the posterior area of the elytra. Two factors, namely the currents produced by the femora, and the presence of small tubercles on the anterior borders of the elytra, probably reduce significantly the tendency of the bubble to be swept away from the beetle. The long axes of the flattened femora of the front and middle legs slope upwards at a fairly sharp angle from their attachments to the trochanters to their attachments to the tibiae, while the short axes slope backwards from the ventral to the dorsal edges. As a result, water meeting the anterior aspect of the femora is deflected dorsally over the elytra, and towards the mid-line. The lateral currents thus produced by the femora on each side of the beetle meet above the elytra to form a dorsal median current which tends to move away dorsally from the elytra of the beetle. The upward movement of this current tends to deflect the main horizontal current passing over the beetle, and thus gives some protection to the anterior parts of the respiratory bubble. Narrow horizontal keels along the edges of the pronotum and elytra ensure that the lateral currents break away cleanly from the body of the beetle, and do not themselves destroy the respiratory bubble. The presence of the deflecting currents was demonstrated by placing the beetles in shallow layers of fast-flowing water that were not quite deep enough to completely cover them. The dorsal median current was then seen as a small jet of water that was thrown clear of the beetle, and passed backwards over the elytra. Any increase in the speed of the main current automatically increased the height to which this dorsal current was thrown.

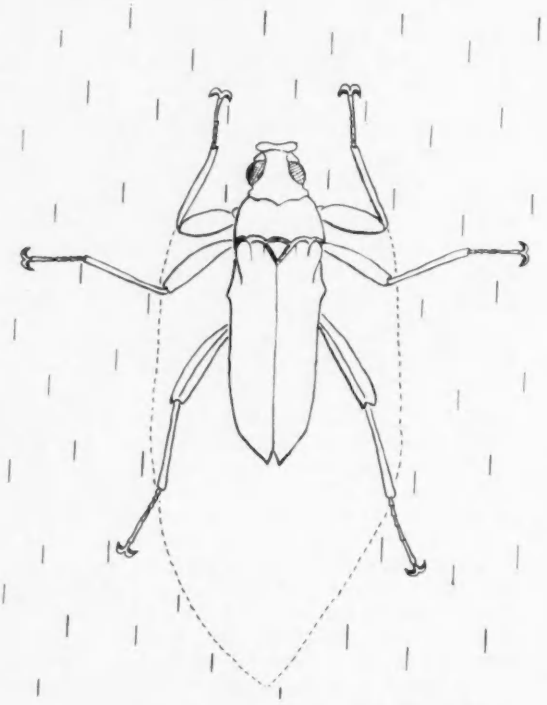

FIG. 1. Diagram to show the position of the respiratory bubble when the beetle has taken up its normal feeding and resting position. The beetle is facing the oncoming current and the approximate area occupied by the bubble is enclosed by the dotted line and the femora of the fore legs.

The tuberosities along the anterior border of the elytra appear to check the horizontal flow of water along the surface of the beetle, and impart a slight vertical component to its direction of flow.

Both the dorsal and ventral edges of the fore femora are provided with sharp ridges, the posterior sides of which make a large angle with the passing current. This ensures that the water breaks away cleanly from the limb at its widest point, and minimizes the tendency of the

water to creep round onto the posterior surface of the limb. Further protection of the bubble is provided by a row of hydrophobe bristles along the dorsal ridge of each femur.

THE TEMPORARY NATURE OF THE BUBBLE IN SLOWLY-MOVING WATER

The following experiment indicated that, when the beetle was immersed in slowly-moving, air-saturated water, the respiratory bubble was temporary in nature.

Ten beetles were narcotized with ether, and each was then attached to a rigid glass fibre, using "Durofix" diluted with amyl acetate as an adhesive. The beetles were then divided into two groups, each of five beetles, and immersed to a depth of 2½ inches in a tank of water. The two groups were about 6 inches apart. A fine aquarium aeration diffuser was placed beneath one group (A), and maintained in continuous operation so that these beetles had a constant supply of air bubbles throughout the experiment, and acted as a control. The other group of beetles was allowed to acquire the largest bubbles that they could hold at the beginning of the experiment but thereafter had to depend on air dissolved in the water. The depth of water in the tank was about eight inches, the diffuser being operated from the floor of the tank. The two groups of beetles were kept under observation and the following results were obtained:—

GROUP A. Beetles in air bubbles from aeration diffuser.

In 2 hours. All beetles responded vigorously when touched with a glass fibre.

In 3 hours. A similar response obtained.

In 20 hours. One beetle had escaped, but the four remaining beetles still responded vigorously.

In 44 hours. Two more beetles had escaped, but the two remaining still responded vigorously.

The diffuser was now moved over to the other side of the tank so that the beetles, although immersed in circulating air-saturated water, no longer received the diffuser bubbles. Within the next six hours the respiratory bubbles of both beetles had disappeared, and the beetles were dead.

GROUP B. Beetles in slowly circulating, air-saturated water.

In 2 hours. The respiratory bubbles were reduced in size, and the beetles responded to the glass fibre less vigorously than did those in Group A.

In 3½ hours. Air bubbles were much reduced in size, and the beetles were being wetted by the water. Four of the five beetles did not respond visibly to the glass fibre, and were apparently dead. The fifth responded weakly.

In 6½ hours. All five beetles were apparently dead, and completely wetted by the water, except on the ventral surface.

The temperature on the first day of the experiment was 30° C at 4.00 p.m., and it is likely that this represented a maximum, and that during the experiment it would have varied between 27° C and 30° C. Temperatures, recorded in the river from which the beetles were obtained, varied between 26.5° C. and 28° C., and the experiment was, therefore, conducted at temperatures comparable with those encountered by the beetles in their natural habitat. The sheen, which persisted on the ventral surface of the beetle for some hours after death, was due to a layer of air entrapped by the hydrophobe hairs which were very numerous in this region. It seemed quite certain that, under the conditions of the experiment, the bubble could only support the life of the beetle for some three to six hours, and this was confirmed several times in later experiments. No contrary results were obtained.

THE EFFECTIVENESS OF THE BUBBLE AS A PHYSICAL GILL WHEN RENDERED PERMANENT BY THE PERIODICAL ADDITION OF NITROGEN

It has already been suggested that in fast-flowing water the respiratory bubble of *P. tuberosus* was permanent and would act, when necessary, as a permanent physical gill. It seemed desirable, however, to confirm experimentally that a bubble of the size normally carried by the beetle could, in fact, function as an effective physical gill provided that its volume was maintained. In a simple experiment it was shown that, if the volume of the respiratory bubble were maintained by the addition of Nitrogen, then the bubble was able to act as an adequate physical gill to support the life of a beetle immersed in air-saturated slowly circulating water.

EFFECT OF FAST-FLOWING WATER ON THE SURVIVAL OF THE BEETLES

In order to investigate the properties of the respiratory bubble in fast-flowing water, a series of experiments was carried out using the apparatus shown in Fig. 2.

Tap water entering this apparatus was aerated by allowing it to pass through a metal filter-pump (J) which projected into a glass cylinder (K). From this cylinder the water overflowed into the upper glass supply tank (A), and thence into the experimental tank (B) through a glass siphon (E). Before entering the siphon, the water permeated through a double screen of linen (C) which prevented any small air bubbles passing over with the water. The flow of water to the experimental tank was controlled by spring and screw clips (F). The lower end of the siphon pierced a large cork (G) to which was attached a cork platform (H). The beetles used in the experiments were attached to this platform.

Several methods of attaching the beetles to the platform were tried, but only the following proved satisfactory. The beetle was narcotized with ether, and a thin nylon thread was attached

to its ventral surface, using "Durofix" diluted with amyl acetate as an adhesive. The thread was drawn through a hole in a small piece of Bristol Board, and fastened to the underside of the Bristol Board with "Durofix". By this means, it was possible to prevent the beetle walking away, and yet allow it sufficient freedom to move its legs and "preen" itself. Two or three beetles were fastened in this manner to a strip of Bristol Board, which was then pinned to the cork platform in the experimental tank. Only one of these beetles would actually be in the current of water issuing from the siphon.

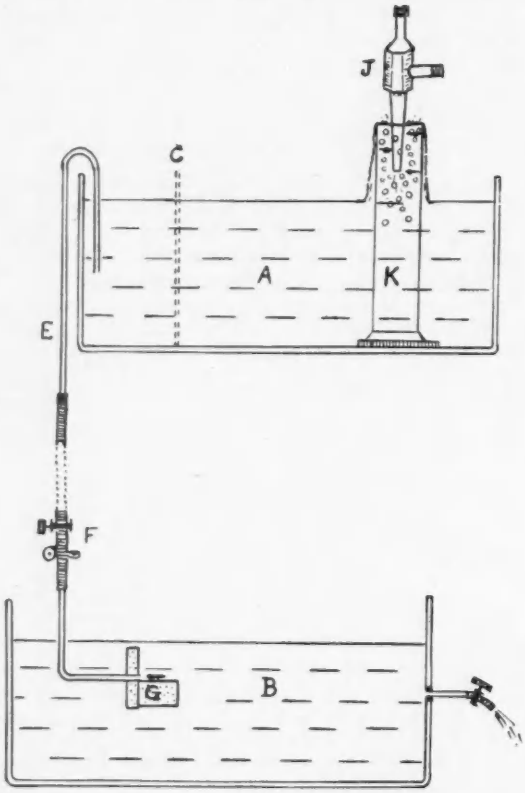

FIG. 2. Diagram of apparatus used for experiments that required running water. In the final experiments water was recirculated through the apparatus by means of a small pump, and the filter pump aerator was eliminated.

A. Supply tank.
B. Experimental tank, fitted with controlled exit tube.
C. Filter to prevent small air bubbles passing to siphon.
E. Siphon conveying water to experimental tank.
F. Clips to control flow of water through siphon.
G. Cork and cork platform on which beetles were placed during experiments.
J. Filter pump for aeration of water supply.
K. Glass cylinder.

In any one experiment it was desirable that the beetles used should commence with bubbles of approximately the same size. This was accomplished by keeping the card well below the surface of the water, and moving it in such a way that each beetle was, in turn, brought into the current of water issuing from the siphon. The beetle soon came to rest facing the current, and air was then introduced into the current of water as it issued from the siphon. The beetle was thus surrounded temporarily by a stream of air bubbles, and was able to acquire the maximum sized bubble that it could hold. When each beetle had been thus provided with a bubble, the card holding them was pinned in position on the cork platform. One of the beetles lay in front of the siphon and received the full force of the current. The other beetle (s) acted as a control experiment, lying in the slowly moving water outside the current. Seven experiments were carried out to compare the survival of beetles in the current with that of those outside the current. The results of five of these experiments are given in Table I. The other two experiments were not completed owing to failures in the water supply. At the end of each experiment there appeared to be no change in the size of the bubble, or of the vigour, of the beetle in the current. On the other hand, during the experiment the beetles outside the current slowly lost their bubbles, and then died. Difficulties with the water supply prevented the duration of the experiments being extended beyond those times given in Table I. These experiments indicated clearly, however, that while the beetle is in fast-flowing water there is little, if any, deterioration in the respiratory quality of the bubble.

TABLE I

TIMES OF SURVIVAL OF BEETLES IN THE EXPERIMENTAL CURRENT COMPARED WITH THOSE OF BEETLES LYING OUTSIDE THE CURRENT

EXPERIMENT No.	SURVIVAL OF BEETLES, IN HOURS	
	In Current	Not in Current
1	> 4½	<3½
2	>11¼	<5¾
		<4½
3	> 8	<8
4	> 8½	<5¾
5	>11½	<6¾

On two occasions during these experiments beetles with much reduced bubbles were observed to regain normal bubbles when in the current of water.

On the first occasion the beetle placed in the current persisted in sitting "the wrong way

round" at the beginning of the experiment. The following observations were made on this beetle.

9:30 a.m. Experiment commenced. The beetle soon came to rest, but was facing downstream.

10:10 a.m. The beetle was still facing downstream, and its bubble had been swept away by the current of water.

10:40 a.m. The beetle had moved, and was more or less facing the current, making an angle of approximately 30° with the direction of flow. Two small bubbles had appeared on the elytra.

12:00 noon. The beetle was still in this position.

12:30 p.m. The bubbles on the elytra were increasing in size and number, and were tending to coalesce.

12:50 p.m. The bubbles on the elytra had coalesced to form a respiratory bubble projecting well beyond the the elytra. Bubbles were appearing on the femora and on the side of the prothorax away from the current.

1:35 p.m. The entire dorsal surface was covered by a bubble.

3:20 p.m. An apparently full-sized bubble had developed on the beetle, and covered the elytra, prothorax, and the usual segments of the limbs. The beetle was strongly active when disturbed. By this time the two control beetles, that were not in the current, had died.

During another experiment, the beetle in the current escaped rather late in the experiment, by which time the bubbles on the control beetles had almost disappeared. One of these control beetles was then transferred to the current, and in less than two hours it had reacquired a normal trailing bubble.

THE "AEROFOIL" PRINCIPLE AS APPLIED TO THE RESPIRATION OF POTOMODYTES

Hinton (1951) has suggested that a degree of supersaturation may occur in running water as a result of small bubbles of air being carried below the surface, and then being dissolved under pressure of a small head of water. This slight supersaturation might prove sufficient to transform a temporary physical gill of the bubble type into a semi-permanent physical gill. That such a mechanism is unlikely to play an important part in the respiration of *Potamodytes* is shown by a consideration of the first experiments described in this paper. In these experiments, with the limited amount of water in the tank being continuously aerated from below by the diffuser, the conditions were apparently much more favourable to supersaturation than were those in the river from which the beetles were taken. Yet the respiratory bubbles of the beetles dissolved away, and the beetles were dead, within 3 to 6 hours. Chemical analysis of samples of water taken from the stream indicated that it contained an amount of oxygen equivalent to that which would be present if it were saturated with air. The method of determination would not, however, have detected a *slight* supersaturation.

The following hypothesis provided a possible explanation of the permanent nature of the bubble of *P. tuberosus* in air-saturated running water. The principle involved is most familiar in its application to the design of aeroplane wings. When a fluid stream flows past an immersed object the stream lines become crowded together (Fig. 3). Since the amount of fluid flowing between adjacent streamlines per unit time remains constant, irrespective of the distance separating them, it follows that the velocity of fluid flow in the region of the narrow crowded streamlines is greater than in the main flow of the fluid. In any region where the velocity of fluid flow is higher than in neighbouring regions there is a reduction in pressure according to the Bernouilli equation, $p + \frac{1}{2}v^2 = a$ constant. Applying this principle to the respiration of *Potamodytes* it seemed reasonable to suppose that the bubble would be in contact with water flowing at a faster rate than in the main stream and, therefore, under a relatively reduced pressure. This reduced pressure would

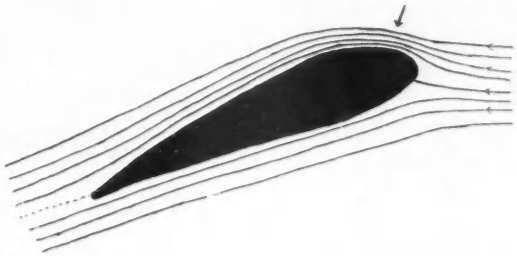

FIG. 3. Diagram showing the streamlines of flow past a lifting aerofoil (after Piercy, Elementary Dynamics). The arrow indicates the region of crowded streamlines, this being also the region of least pressure.

be communicated to the respiratory bubble. If the water had been saturated with air at atmospheric pressure, then on entering the region of reduced pressure adjacent to the beetle it would become temporarily supersaturated. As a result, air might be expected to pass continuously from the water into the bubble. Such a hypothesis, if correct, would account for the increase in size of the respiratory bubble which occurred on the two occasions noted in this paper.

THE PRESSURE IN THE RESPIRATORY BUBBLE

Further experimental work, designed to test the hypothesis suggested above, was limited by the laboratory facilities available. Since, however, the hypothesis was based on a reduction of pressure in the respiratory bubble, it seemed advisable to confirm experimentally that such a reduction of pressure did occur.

A certain amount of difficulty was encountered in determining the pressure inside the air bubble, but the following technique proved moderately successful. An anesthetised beetle was fastened lengthways to a large matchstick, its ventral surface being fastened to the matchstick with

"Durofix". The beetle thus had very little freedom for movement, and it was possible to insert a very fine waxed glass tube into the subelytral space of the beetle, the glass tube itself also being firmly fastened to the matchstick. The subelytral space was always in direct communication with the respiratory bubble, and pressure changes in the bubble could, therefore, be detected by attaching the waxed glass tube to a simple water manometer. The pressure changes recorded in this manner were small, and it was necessary to use a manometer with a sloping arm that magnified the vertical movement of the water. On this manometer a vertical rise of 1.0 cms., was represented by a fluid movement of 17.9 cms., along the sloping arm. Readings were taken at various current speeds, the current speed being determined by removal of the beetle and the substitution of a Pitot tube. The beetles were submerged under a constant head of about 1 cm., of water. The results obtained are set out in Table 2 and shown graphically in Fig. 4. In each case before the bubble pressure was recorded, air was introduced into the current of water before it reached the beetle. This ensured that the bubble was of a size that was in equilbrium with the particular current speed under consideration. It will be noted that the pressure recorded in the bubble did not fall below that of the atmosphere until the current speed reached about 70 cm. per second. At lower speeds the pressures recorded were either equal to, or above, that of the atmosphere. Both the head of water above the bubble, and the surface tension forces tending to contract the bubble, would have the effect of raising the pressure above atmospheric at the lower current velocities. It will be noted also that the results obtained from any one experiment do not lie on a smooth curve, and it seems probable that these irregularities arose as a result of the difficulty experienced in placing the Pitot tube in exactly the same position that the beetle had occupied. Finally, it should be pointed out that the mathematical relationship of the actual current velocity to the reduction in pressure of the bubble will be

TABLE II

RESULTS OF SIX EXPERIMENTS CARRIED OUT TO DETERMINE THE EFFECT OF THE VELOCITY OF THE WATER CURRENT ON THE INTERNAL PRESSURE OF THE RESPIRATORY BUBBLE OF ADULT *Potamodytes*

EXPERIMENT NO.	REDUCTION IN PRESSURE	CURRENT SPEED (cms. per sec)
1	3.28	152
	2.19	138
	0.44	108
	0.22	104
	−0.11	99
2	0	82
	0.82	96
	1.53	117
	1.92	155
3	0	76
	0.87	92
	0.98	122
	2.41	178
	1.09	128
4	3.72	191
	3.05	156
	1.86	153
	1.04	121
	0.16	101
5	0	66
	0.05	90
	0.55	111
	0.98	140
	3.05	162
	3.50	183
	2.63	153
6	0	90
	0.27	113
	0.66	124
	1.48	154
	1.27	134
	3.83	184
	2.30	163
	2.84	153

Reduction in Pressure Expressed in MMS. Water.

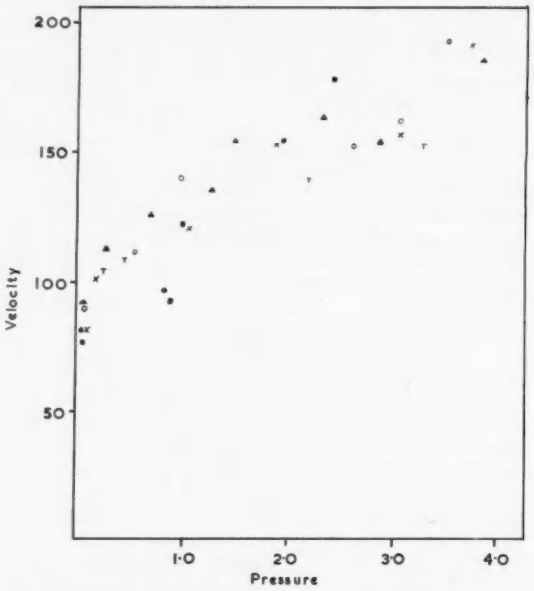

FIG. 4. The relationship between the velocity of the water current and the reduction in the internal pressure of the respiratory bubble of *Potamodytes*.

The velocity of the water is expressed in cms. per second.

The internal pressure of the bubble is recorded as mm. water *below* atmospheric pressure.

complicated by the change of shape that occurs in the bubble with change of current velocity.

SUMMARY

1. The respiratory bubble of the adult beetle is described. It is maintained in position partly by the non-wettable properties of the surface of the beetle, and partly by the structure of the beetle.

2. Evidence is presented that, in fast-flowing, air-saturated water, the respiratory bubble can act as a permanent physical gill.

3. As an explanation it is suggested that, in fast flowing water, regions of reduced pressure are created in the neighborhood of the respiratory bubble. The bubble is, therefore, at a pressure somewhat less than atmospheric, and will consequently tend to withdraw air from water that has been saturated at atmospheric pressure.

4. This hypothesis gains a considerable support from the experimental demonstration that the pressure of the respiratory bubble falls below that of the atmosphere when the beetle is placed in fast-flowing water.

ACKNOWLEDGEMENTS

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A CONTRIBUTION TOWARD A MONOGRAPH OF THE SCATOPSIDAE (DIPTERA) PART II, THE GENERA RHEGMOCLEMINA ENDERLEIN, PARASCATOPSE N. G., AND A NEW SPECIES OF RHEGMOCLEMA[1]

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INTRODUCTION

In the course of this study three hitherto undescribed species were discovered in the material lent to me by the U. S. National Museum. These species from Florida, Mississippi and southern California form a natural group closely related to *Rhegmoclema* Enderlein considered in the preceding paper in this series (Cook, 1955) and *Rhegmoclemina* Enderlein discussed in the present paper. This group will be herein described as a new genus, *Parascatopse*. The close relationship of these three genera is evident from the following characteristics shared by the included species examined:

1. Maxillary palpi short and somewhat ovoid in form.
2. Vein Cu_2 bearing at least a few macrosetae (one exception, *R. abruptinervis* (Duda)).
3. Vein Cu_2 with two right angled bends along its course.
4. Some species in each genus with 12 antennal segments.
5. Pedicel of haltere without macrosetae.
6. Females with 8 pairs of abdominal spiracles.
7. Female terminalia with but a single pair of appendages (probably cerci) articulated to tergite 8 or fused to tergite 8; in the latter case tergite 8 longitudinally divided and the tergite and cerci simulating the cerci and appearing to articulate to segment 7 (*Rhegmoclema*).

These three genera can be conveniently considered to be a tribe, Rhegmoclemini, separable from other genera heretofore included in the Scatopsini by the characteristics noted. The three genera within this tribe can be separated by the following key:

1. At least 1 macroseta present on M_1 and M_2 (usually more); M_1 incomplete at base (except in *R. rufithorax*) ..... **Rhegmoclema**
1a. No macrosetae on M_1 or M_2; M_1 always complete.. 2
2. Seventh sternite of the males distinctly shield-shaped (Fig. 2); a more or less distinct row of supra-alar setae..... **Rhegmoclemina**
2a. Seventh sternite of males not shield-shaped (Fig. 4D, F, H); no distinct supra-alar row of setae..... **Parascatopse** new genus

The genus *Rhegmoclemina* was established by Enderlein (1936) to include the single species

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Scatopse vaginata Lundström from northern Europe. Enderlein's characterization of this genus is contained in a key to the genera of central Europe, and no separate description of the genus has been presented. By extracting the appropriate parts of each of the dichotomies (omitting one obvious typographical error[2]), we arrive at the following summary of characters for the genus: wings normally developed; a clear fold present between M and Cu; macrotrichia lacking on the hind veins[3] and on the wing surface; M_1 not reduced basally; pterostigma wide; antennae 9- to 10-segmented; Cu_2 strongly bent twice, forming a Z-shaped vein; end parts of Cu_1 and Cu_2 lacking or very faint; base of the M fork mostly shorter than the M fork, at most of equal length; cell M_1 not constricted distad of the middle; section of the costa between R_1 and R_3 mostly very short.

Despite this rather inadequate description, the designation of *Scatopse vaginata* as the type species makes possible the recognition of the group. Lundström's original description (1910) includes a small drawing of the dorsal aspect of the male genitalia (erroneously identified as the female) and a drawing of the wing. Duda (1928) examined the type and quite adequately redescribed the species based on that and several other specimens. In addition, Duda also included drawings of a wing and the lateral aspect of the male genitalia. These illustrations and descriptions are sufficient to establish the very close affinity of the several species to be considered in this paper with the type species of this genus. Of the species previously described, *Rhegmoclema bimaculata* Melander, R. *scrobicollis* Melander, *Scatopse clavicrus* Duda and *Scatopse abruptinervis* Duda belong in this genus. I have not seen other described species but from descriptions and illustrations it seems probable that *Scatopse forcipata* Duda from Africa, *S. trichioneura* Duda from Costa Rica and *Scatopse constricta* Edwards from Chile belong to this genus also. In addition to these, four new world species belonging to this genus will be described herein as new.

Enderlein's scatopsid genera have been slow to gain acceptance; in fact they have been either rejected outright (Duda, 1928) or accepted in part as subgenera (Edwards, 1930). It seems evident, however, that this genus is a natural and valid group whatever the anatomical bases for its original establishment.

As far as is known at present, this genus is represented in northern Europe by the type species, in North America by six species, in the West Indies, Central and South America by five species and in Africa by one species.

Nothing is known of the immature stages nor the biology of this group aside from the record of Edwards (1930) stating that *Scatopse constricta* was collected in a rotten log in company with termites.

The name *Rhegmoclemina* is rather unfortunate because of its similarity to the name of the most closely related genus, *Rhegmoclema*, but the name has been properly proposed and is valid.

Rhegmoclemina Enderlein

Rhegmoclemina Enderlein, 1936. Die Tierwelt Mitteleuropas, Bd. 6: Lief. 2, Inseckten 3: p. 55. Type *Scatopse vaginata* Lundström, 1910.

GENERIC DESCRIPTION

This genus can be readily divided into two subgenera one of which will be herein described as new. The known species are somewhat more variable in size than those of *Rhegmoclema* previously described. The total length varies from 1.10 to 2.50 mm. The larger species are apparently confined to the west coast of North America while the smaller species are to be found in southeastern United States and South America. Most of the species are dark brownish black to black with jet black heads, but two specimens representing a species found in Florida and a single specimen representing a species found in the West Indies are of a paler greyish brown color with somewhat darker heads. All of the species are more or less glossy in appearance.

Head: The head is hypognathous, laterally compressed and elongate. The eyes are holoptic in both sexes, confined to the anterior one-half of the head and finely and sparsely pubescent. There are three ocelli on the vertex immediately above the eyes. The antennae are ten- to twelve-segmented in all the known species, somewhat shorter than the head height, of a dull black color and covered with a fine pubescence and a number of short, stout setae. The head capsule is convex behind the eyes and bears scattered, short setae. A complete tentorium is present.

The mouth parts are reduced as in other non-biting Diptera. The maxillary palpi are one-segmented, short, 0.05 to 0.07 mm. long, apically rounded and covered with a fine pubescence and short, stout setae. There is a sensory pit located apically or dorsally on each palp. The labellae are small, palpiform, without pseudotracheae and bearing setae as in the palpi.

Thorax: The thorax is laterally compressed and stoutly sclerotized. The scutum and scutellum bear numerous, short, scattered setae and in addition a few longer setae around the posterior

[2]Enderlein states that the base of M_1 is lacking immediately after the statement that it is not reduced.

[3]This is probably an error of observation if Enderlein saw the specimens, since all new world species have macrosetae on vein Cu_2; he probably saw no specimens but followed the description of Lundström or Duda, neither of whom noted this character.

margin of the scutellum and at each posterolateral corner of the scutum. There is a rather regular row of long, stout, closely spaced setae (the supra-alar setae) on the lateral margin of the scutum just above the wing base. The anterior spiracle is located more or less medially in a triangular sclerite anterior to the anepisternum. This spiracular sclerite bears a variable number of setae scattered around the spiracle. The pronotum has scattered setae. A cluster of small setae is present on the anepisternum immediately anterior to the wing base, but these are neither as stout nor do they form the regular row present in *Rhegmoclema*. An irregular cluster of setae also occurs on the anepimeron immediately beneath the wing base. Two or three stout setae are present beneath the posterior spiracle (subspiracular setae). The postnotal phragma is large as in *Rhegmoclema* and all other members of this family seen.

The wings have the costa and the radius and its branches well sclerotized and pigmented. Veins M and Cu are faint but visible. The costa and radius bear numerous macrosetae in all species. Veins M_1, M_2, and Cu_1 are always without macrosetae. Vein Cu_2 has at least a few macrosetae in most all of the specimens examined. In the typical subgenus the membrane behind Cu_2 bears setae. The whole of the wing membrane is covered with microtrichia. M_1 is always complete, and Cu_2 has either one or two right-angled bends along its course. The fork of M is from 2.25 to 4.75 times as long as the stem of the fork and section 2 of the costal margin (Fig. 3 D, E) is short. The ratio of the length of section two to section three varies from 1 to 4 to 1 to 6.5.

The halteres are covered with microtrichia. The ovate capitulum bears a number of fine setae while the pedicel is bare of setae.

The tarsal segments are rather short and thick and bear numerous setae both fine and stout. A lobe-like, marginally setaceous empodium is present. The claws are simple.

Abdomen: There are seven obvious pregenital segments in both sexes, the males with seven pairs of spiracles and the females with eight. Segment one is shorter than the succeeding segments. There is no reticulate pattern on the cuticle of tergum one in any of the species examined. Tergum 2 in both sexes is divided into two small paired anterior sclerites and a larger median sclerite posteriorly. The terga and sterna are well defined and bear a few scattered setae. Sternite 7 of the males is shield-like in all species (Fig. 2).

Male genitalia: The genitalia of the males fall into two very distinctive types. Since the differences shown in the genitalia are the primary critera for separating this genus into two subgenera, these structures will be described in the subgeneric descriptions. It should be noted here, however, that the male genitalia in most cases are rotated through 180°. This is evident from the fact that the penis is located dorsad of the anus. Tergal structures are therefore located ventrally and vice versa. In one species of the genus an additional tergite has been found folded beneath the seventh tergite. Since this tergite (Fig. 2G) is interposed between tergite seven and the genitalic complex, it must be tergite 8. It was not found in any other species. This would indicate that the male genitalia are composed of segment 9 and succeeding segments exclusively and that segment 8 has in most cases been lost. Edwards (1930) indicated this possibility as noted in the first paper in this series.

The "free" vesica is large and well developed in all members of the genus.

Female genitalia: The female genitalia (Fig. 3A, B) are very similar in both subgenera. They are small and compact as in *Rhegmoclema* but do not, unfortunately, offer any clear-cut specific characters as is the case in that genus. In the present genus, tergite 8 with its spiracles is not divided longitudinally nor are the apparent cerci fused to the tergite as was the case in *Rhegmoclema*. Instead the apparent cerci are articulated to the posterior margin of tergite 8. Segments 9 and 10 are either much reduced or absent. There is a single well-sclerotized spermatheca in all species.

KEY TO THE SUBGENERA

1. Antennae with 10 segments; wing with macrosetae on vein Cu_2 and on the membrane behind Cu_2 ..... **Rhegmoclemina**
1a. Antenna with 12 segments; wing may have a few macrosetae on Cu_2 but never with macrosetae on the membrane behind Cu_2. . **Neorhegmoclemina**

KEY TO THE SPECIES OF SUBGENUS RHEGMOCLEMINA[4]

1. Male genitalia with three posteriorly directed processes dorsally (Fig. 1A, B)..... 2
1a. Male genitalia with two elongate, posteriorly directed processes (Fig. 1C, E)..... 3
2. Male genitalia with a pair of dorsally projecting lateral processes on tergite 9 (Fig. 1A). **bimaculatum**
2a. Male genitalia without such processes (Fig. 1B)... ..... **scrobicollis**. .
3. Tergite 7 of males produced posteriorly, triangular (Fig. 2E)..... **clavicrus**
3a. Tergite 7 of males posteriorly incised (Fig. 2B)..... ..... **melanderi**

KEY TO THE SPECIES OF SUBGENUS NEORHEGMOCLEMINA

1. Male with tergite 7 incised posteriorly (Fig. 2G). Female with a pair of sclerotized pockets on the anterior margin of tergite 7 (Fig. 3C). **bisaccatum**
1a. Tergite 7 without such structures in either sex.... 2

[4]Females are not included in this key for the following reasons: ♀ ♀ of *R. melanderi* are unknown; ♀ ♀ of *R. clavicrus* are only known from description; ♀ ♀ of *R. bimaculatum* and *R. scrobicollis* differ only in relative size and offer no clear key characters.

2. Male with tergite 7 produced posteriorly (Fig. 2H); apodemes of sternite 7 arising medially. Cu_2 without macrosetae. Veins M_1 and M_2 divergent from base..... **abruptinervis**

2a. Males with tergite 7 incised medially (Fig. 2D, F); apodemes of sternite 7 arising laterally. At least a few macrosetae on Cu_2. M_1 and M_2 convergent between origin and wing margin (Fig. 3E)..... 3

3. Size small (1.3 mm.); male genitalia asymmetrical; penis sinuate, apically slender. (Fig. 1G)..... **asymmetricum**

3a. Size large (1.7 mm.); male genitalia symmetrical; penis straight, not reduced apically (Fig. 1F)... **parvum**

Subgenus **Rhegmoclemina** s.s.

All of the species included in this subgenus share the following characteristics: antennae with ten segments; wings with macrosetae on Cu_2 and on the membrane posterior to Cu_2; posterior margin of sternite six with a short row of short, stout setae; sternite seven of the males without particularly conspicuous basal apodemes (Fig. 2A, B, C, E).

Male genitalia: The genitalia (Fig. 1A, B, C, E) are composed of two sclerites primarily. Ventrally, there is a variously modified, somewhat flattened, posteriorly setaceous sclerite which may be assumed to be tergite 9. In *R. bimaculatum* this sclerite is produced posteriorly and dorsally into two prominent, setaceous, finger-like lobes. Dorsally there is a sclerite resembling the whole of the male genitalia in *Rhegmoclema*. From this dorsal (but morphologically ventral) structure there arise two or three long, slender, acute, posteriorly directed processes. The trifurcate condition is present in *R. bimaculatum* and *R. scrobicollis;* the bifurcate condition is present in the type species *R. vaginata* and the other species of this subgenus. The two lateral processes are minutely setaceous apically. These may be the penis valves. Duda (1928) assumed these processes in *R. vaginata* to represent a bifurcate penis. This is doubtful, however, since in all of these species the short, sclerotized penis is visible dorsally at the base of these processes.

Rhegmoclemina (**Rhegmoclemina**) **Bimaculatum** (Melander), new combination

Rhegmoclema bimaculata Melander, 1916. State College of Washington Ag. Exp. Sta. Bull. 130: 14–15, Fig. 14.

This species and that immediately following have been but briefly described by Melander and some additional characteristics should be added.

Males: Total length 1.72 to 2.59 mm. Color dark brownish black to black, shining; head jet black, shining; antennae dull black, segments 1 and 2 brownish; a bright yellow spot on each posteriolateral corner of the scutum; abdomen shining black both dorsally and ventrally, dull laterally; halteres dark grey to brown; empodia yellowish brown; all setae light brown. Maxillary palpi short, 0.068 mm. long. Enlarged supra-alar setae present, in a definite row, 9 to 12 in number; two large subspiracular setae present.

Wings (Fig. 3D) 2.00 to 2.59 mm. long; third section of costa four times as long as the second; M_1 3.5 times as long as M.

Segment 7 of abdomen as in Fig. 2A. Tergite 7 of somewhat variable, sometimes shorter, sometimes more slender and more symmetrical. Genital vesica and apodemes 0.53 mm. long. Male genitalia as in Fig. 1A.

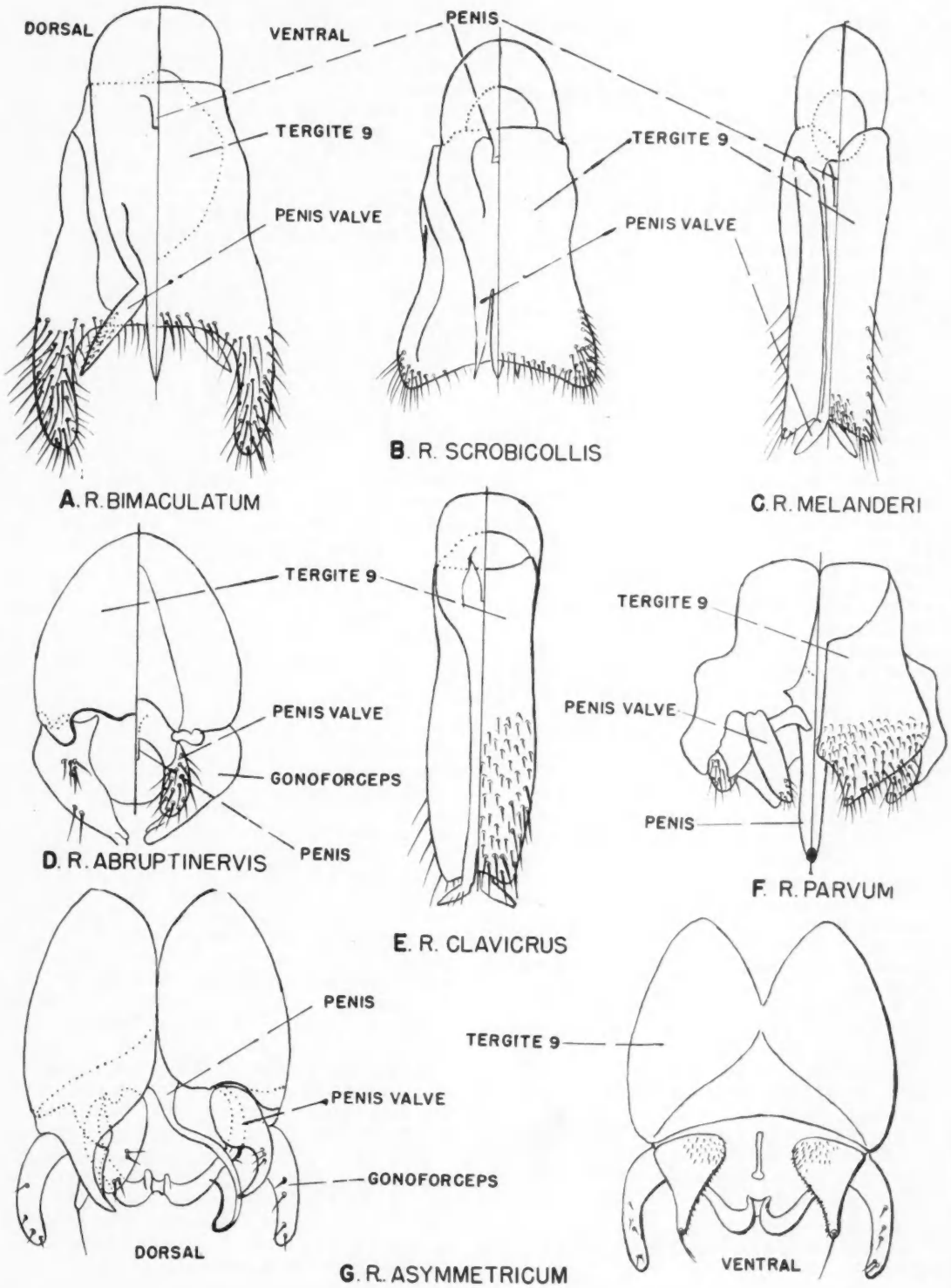
Females: Total length 1.72 to 2.76 mm.; wing length 1.90 to 2.45 mm. Female genitalia dark grey, rather paler than abdomen. Supra-alar setae seven to nine; subspiracular setae one or 2. Otherwise identical with the male in color and chaetotaxy.

The relationship between this species and *R. scrobicollis* will be discussed following the description of the latter species.

From the specimens that have been available for this study, this species is apparently restricted to costal or near-costal areas from San Luis Obispo County, California to Vancouver Island, B. C.—Melander (1916) records a specimen from Sheep Creek, Alaska. Type locality, Quilcene, Washington. Type in the collection of A. L. Melander.

Specimens examined:

California: Asilomar, 6♂♂, 2♀♀, Sept. 28-Oct. 3, 1946; 11♂♂, 6♀♀, Sept. 1–3, 1945; 1♂, Berkeley, June 18, 1907; 1♂, Fortuna, June 20, 1925; 1♀, Half Moon Bay, June 21, 1947; 1♂, 2♀♀, Inverness, Marin County, Aug. 27, 1949; 21♂♂, 18♀♀, Mad River Beach, Humboldt Co., Aug. 12, 1948; 2♂♂, 6♀♀, Monterey, July 17, 1896; 9♂♂, 4♀♀, Sept. 25, 1934; 1♂, 2♀♀, Morro Bay, San Luis Obispo Co., Aug. 9, 1946; 1♂, Pt. San Pedro, San Mateo Co., April 5, 1905; 14♂♂, 6♀♀, Osa Flaca Lake, San Luis Obispo Co., June 22, 1948; 1♀, Pacific Grove, May 7, 1906; 1♂, Redwood City, April 19, 1906; 1♂, 2♀♀, San Francisco, June 18, 1922; 1♂, 1♀, May 13, 1913; 1♂, April 15, 1921 (dunes); 1♀, San Mateo Co., June 17, 1917; 3♂♂, Smith River, July 17, 1930. *Oregon:* 1♀, Humbug State Park, Aug. 7, 1940. *Washington:* 1♂, 1♀, Canyon Creek, July 26-28; 4♀♀, Granite Falls, July 25, 1925; 1♀, Guemes Island, July 13, 1905; 1♂, 1♀, Ilwaco, June 28, 1925; 5♂♂, 1♀, July, 1917; 1♀, July 1918; 2♂♂, Lake Crescent, Piedmont, July 26, 1917; 1♂, Lake Cushman, July 22, 1927; 1♂, Lilliwaup, July 23, 1927; 2♂♂, 1♀, Mt. Baker, Nooksack River, Aug. 11, 1925; 1♂, 2♀♀, Olympia, Aug. 6, 1921; 1♂, Pluvias, July 16, 1922; 1♀, Potlatch, Hoods Canal, July 28, 1917; 1♀, Quilcene, Aug. 11, 1921; 1♂, Seattle, June 16, 1920; 1♂, no date; 11♂♂, 1♀, Shelton, Walkers Pk., July 21, 1917; 2♂♂, 1♀, Sultan, Aug. 1, 1917; 6♂♂, 2♀♀, Tacoma, July 23, 1915; 4♂♂, 1♀, July 29, 1917; 1♂, 2♀♀, no date; 14♂♂, 6♀♀, Tualip, Aug.


DORSAL
VENTRAL
TERGITE 9
PENIS VALVE
A. R. BIMACULATUM
PENIS
TERGITE 9
PENIS VALVE
B. R. SCROBICOLLIS
TERGITE 9
PENIS VALVE
C. R. MELANDERI
TERGITE 9
PENIS VALVE
GONOFORCEPS
PENIS
D. R. ABRUPTINERVIS
E. R. CLAVICRUS
TERGITE 9
PENIS VALVE
PENIS
F. R. PARVUM
PENIS
PENIS VALVE
GONOFORCEPS
DORSAL
G. R. ASYMMETRICUM
TERGITE 9
VENTRAL

3, 1917. *British Columbia:* 1♀, Vancouver, Aug. 8, 1917; 1♂, Vancouver Island, Mill Bay, July 12, 1924.

Rhegmoclemina (Rhegmoclemina) scrobicollis (Melander), new combination

Rhegmoclema scrobicollis Melander, 1916. State College of Washington Ag. Exp. Sta. Bull. 130: 15, Fig. 16.

Males: Total length 1.65 to 2.34 mm. Color as in *R. bimaculatum* except scarcely shining and spot at posterior lateral corner of scutum smaller and varying from pale yellow to pale brown. Maxillary palpi short, 0.068 mm. Enlarged supra-alar setae present in a definite row but interspersed with smaller setae, 7 to 10 in number; 2 large subspiracular setae.

Wings 1.58 to 1.96 mm. long; third section of costal margin somewhat more than 4 times as long as second; M_1 3.5 times as long as M.

Segment 7 of abdomen as in Fig. 2C; tergite 7 always triangular. Genital vesica and apodemes 0.51 mm. long. Male genitalia as in Fig. 1B.

Females: Total length 1.58 to 1.96 mm. Wing length 1.45 to 1.79 mm. Female genitalia concolorous with abdomen. Female genitalia as in Fig. 3A. Enlarged supra-alar setae 8; subspiracular setae 2. Otherwise identical in color and chaetotaxy with the males.

This species is close to *R. bimaculatum* but differs constantly in the male genitalia and tends to be smaller in total size and in wing length. There is no overlap nor intergradation in size in those specimens of these two species that I have had available for examination from the region in which these two species coexist both spatially and temporally. Further, there is no apparent intergradation in the structure of the male genitalia in this area, although one male of *R. bimaculatum* has been seen from Ilwaco, Washington in which the posteriorly directed processes of tergite 9 are much reduced, thus approaching the genitalia of *R. scrobicollis*. Since intergradation does not occur in the area of contact, these two forms are considered to be distinct species. According to the specimens available, this species is distributed along the California coast from San Luis Obispo County to San Diego. Type in the collection of A. L. Melander. Type locality, San Diego, California. Specimens examined:

California: 1♂, San Diego Co., March 11, 1897, W. M. Wheeler (This specimen from the American Museum of Natural History has identical data with those of the holotype); 4♂♂, 2♀♀, Morro Bay, Aug. 30, 1945; 6♂♂, 4♀♀, Osa Flaca Lake, San Luis Obispo Co., June 22, 1948; 4♂♂, 1♀, Carpenteria, Aug. 11, 1950.

Rhegmoclemina (Rhegmoclemina) melanderi n. sp.

Males: Total length (from slide mounted specimens) approximately 2.00 mm. to 2.50 mm. Color dark grey brown to black, shining; head jet black, shining; antennae dull black; a pale somewhat yellowish spot at the posterolateral corners of the scutum; abdomen dark brown to black both dorsally and ventrally, dull laterally; halteres grey to dark grey; empodia yellowish brown; all setae brown. Maxillary palpi shorter than in the two preceding species, 0.051 to 0.060 mm. long. Enlarged supra-alar setae in a definite row, 10 to 12 present followed posteriorly by a double row of 3 or 4 pairs. Subspiracular setae, 2 large or 2 large and 2 small.

Wings 1.72 to 2.24 mm. long, proportioned as in Fig. 3D. Specimens from Ontario and Yellowstone National Park, Wyoming with only 2 or 3 setae on the membrane behind Cu_2; specimens from California with more numerous setae on the membrane as in Fig. 3D. Section 3 of the costal margin 4.75 to 5 times as long as section 2; M_1 2.25 to 3 times as long as M.

Segment 7 of the abdomen as in Fig. 2B. Sternite 7 somewhat variable, the posterior margin may be more angulate than rounded and the median constriction may not be evident. Genital vesica and apodemes 0.46 to 0.60 mm. long. Male genitalia as in Fig. 1C.

Female: Unknown.

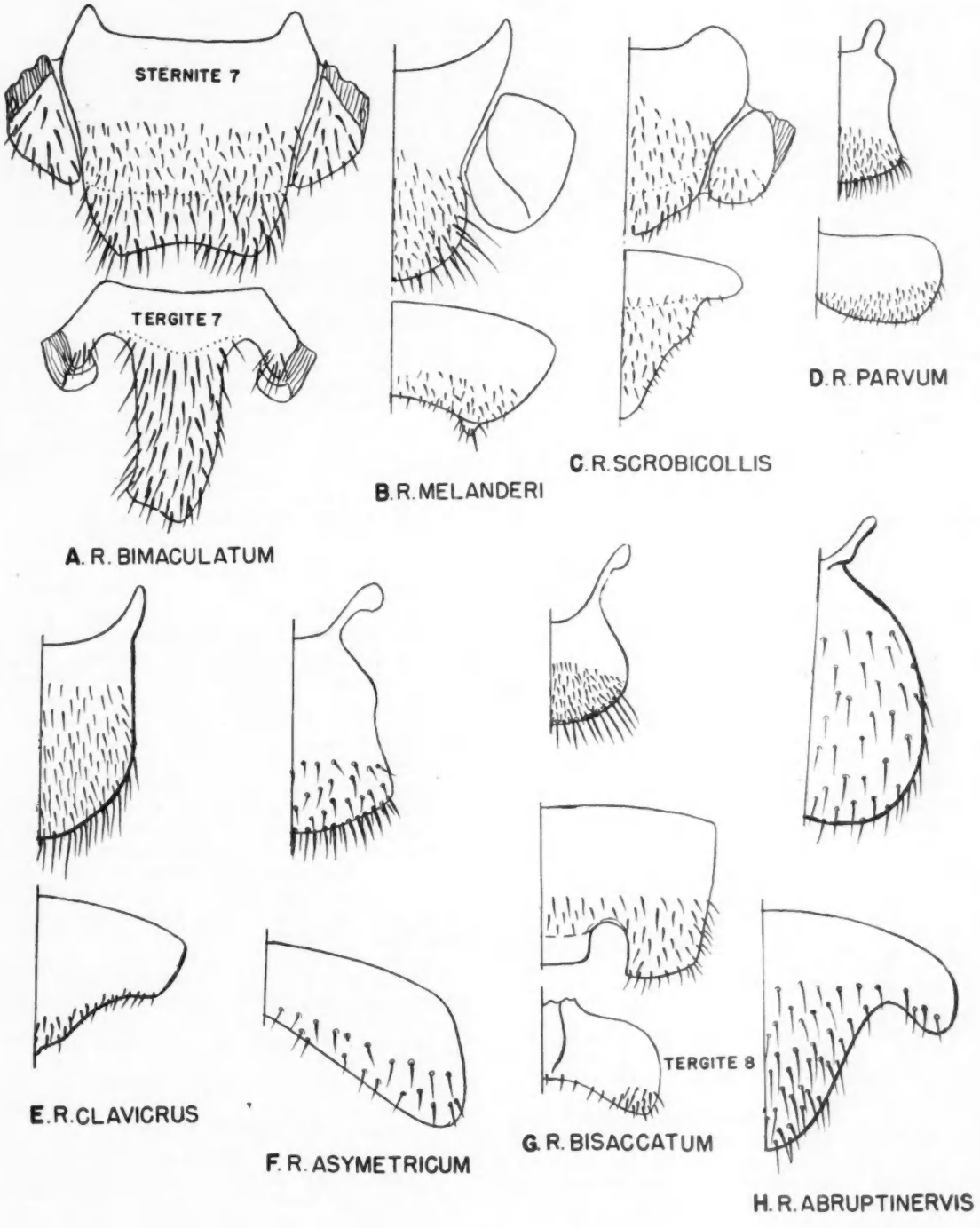
The illustrations are of the holotype. The holotype is the smallest of the specimens available and the minimum measurements given in each instance are those of the holotype.

This species is very close to *R. vaginata* (Lundström), the type species of the genus, in regard to the structure of the male genitalia. It differs from *R. vaginata* in the relative lengths of the second and third sections of the costal margin and in the length of M relative to M_1. In *R. vaginata* these are: third section of costal margin 3.75 times as long as second; M_1 3.25 times longer than M. These are the only evident differences from examination of the descriptions and illustrations of Lundström and Duda (1928). Since all other North American species in this group with the exception of two cosmopolitan species heretofore regarded as conspecific with European species have proven to be distinct, this species will also be treated as distinct until evidence to the contrary is available.

Holotype: ♂, Arroyo Seco R.S., Monterey County, *California*, July 1, 1948, stream margin. W. W. Wirth. Type in the United States National Museum.

Paratypes: 1♂, Fales Hot Springs, Mono Co., *California*, June 7, 1948. W. W. Wirth; 1♂, Indian Creek, Yellowstone Park, *Wyoming*, July 8, 1923. A. L. Melander (Melander Collection). 1♂, Vineland Station, *Ontario*, June 28, 1937 (Canadian National Collections).

All specimens slide-mounted.


STERNITE 7
TERGITE 7
A. R. BIMACULATUM
B. R. MELANDERI
C. R. SCROBICOLLIS
D. R. PARVUM
E. R. CLAVICRUS
F. R. ASYMETRICUM
TERGITE 8
G. R. BISACCATUM
H. R. ABRUPTINERVIS

Rhegmoclemina (Rhegmoclemina) clavicrus (Duda), new combination

Scatopse clavicrus Duda, 1928. Konowia, 7: 282–283, Tafelfig. 4.

This species is based on a single female specimen from Suiza de Turrialba, Costa Rica, May 20, 1921. The type (*fide* Duda) is in the Hungarian National Museum. In the material kindly loaned to me by Dr. A. L. Melander there is a single male specimen also from Suiza de Turrialba, Costa Rica, collected in July by Pablo Schild. Although this specimen is a male and the type a female the striking similarity between the wing of the male and that of the female and the close agreement of the male with the description of Duda indicate that these are conspecific.

Male: Total length (from slide mounted specimen) approximately 2.00 mm. Color black, shining; head jet black, shining; antennae dull black; a somewhat paler spot at the posterolateral corner of the scutum; abdomen shining black dorsally and ventrally; halteres dark grey; empodia yellowish. Maxillary palpi slightly longer than in the preceding species, 0.08 mm. long. Enlarged supra-alar setae in a definite row, 14 present plus a double row of 4 pairs posteriorly. Subspiracular setae 3.

Wings 1.90 mm. long. Macrosetae are present on the membrane behind Cu_2 as in *R. bimaculatum*. Section 3 of costal margin 4.6 times as long as section 2; vein M_1 2.75 times as long as M.

Segment 7 of abdomen as in Plate 2E. Genital vesica and apodemes 0.39 mm. long. Male genitalia as in Fig. 1E.

Female: This has been described by Duda, and having seen no female specimens I can add nothing to that description.

This species is very close to *R. melanderi* but differs in the form of tergite 7, chaetotaxy and proportions of the male genitalia.

Specimen examined: 1♂, Suiza de Turrialba, Costa Rica, July. Pablo Schild (no further data).

Neorhegmoclemina, New Subgenus

All of the species included in this subgenus share the following characteristics: antennae with twelve segments; wings with or without a few macrosetae on Cu_2 but never with macrosetae on the membrane behind Cu_2; posterior margin of sternite six without a row of short stout setae, one species with two short setae, the remainder with none; sternite seven of the males with conspicuous basal apodemes (Fig. 2D, F, G, H).

Male genitalia: The genitalia (Fig. 1D, F, G) are relatively much shorter than in the typical subgenus. The tergite is divided longitudinally and is rather setaceous posteriorly. Articulating to this structure laterally is a pair of stoutly sclerotized, larger or smaller processes which may be the gonocoxites which are termed here the gonoforceps. No attempt will be made here to determine the homologies of the parts of the male genitalia or to apply the correct morphological terms to them. Examination of Fig. 1, particularly G and H, should indicate the complexity of the structures. In *R. parvum* there are three pairs of articulated structures, while in *R. abruptinervis* only two pairs can be observed. In *R. asymetricum*, there are more appendages on one side than on the other. This is also true of *R. bisaccatum*, which is not illustrated. The question of the morphology of the male genitalia of this group will be deferred to a subsequent paper.

Type species: **Rhegmoclemina (Neorhegmoclemina) parvum** n. sp.

Another species should be included in this subgenus in addition to those described in this paper. This is *R. constricta* (Edwards) (1930), Diptera of Patagonia and South Chili, Part 2, fasc. 3: 96–97. The subgeneric position of *R. forcipata* (Duda) and *R. trichioneura* (Duda) (Konowia, 1: 260 *et. seq.*), cannot be ascertained as the descriptions are inadequate.

Rhegmoclemina (Neorhegmoclemina) parvum, n. sp.

Male: Total length approximately 1.70 mm. Color dark brown, dull; head dark brown, shining; legs dark brown except tarsi light brown; abdomen black on anterior four tergites, lighter grey brown posteriorly and ventrally, dull; halteres dark grey; setae yellowish brown. Maxillary palpi quite short, 0.05 mm. long. Enlarged supra-alar setae present in a definite row, 15 in number; subspiracular setae 3.

Wings 1.45 mm. long. Section 3 of costal margin 6.5 times as long as section 2; M_1 2.75 times as long as M. The fork of vein M (veins M_1 and M_2) is constricted midway between its origin and the wing margin as in *R. asymmetricum* (Fig. 3E). Macrosetae are present on vein Cu_2.

Segment 7 of abdomen as in Fig. 2D. Genital vesica and apodemes 0.34 mm. long. Male genitalia as in Fig. 1F.

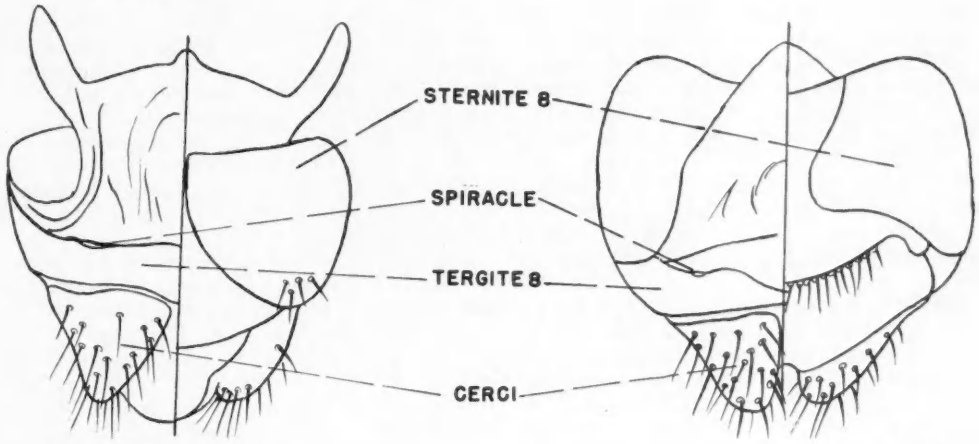
Female: Total length approximately 1.70 mm; wing length 1.31 mm. Supra-alar setae 11; subspiracular setae 2. Otherwise identical with the male in color and chaetotaxy.

Holotype: ♂, Kilbourne, Louisiana, May 4, 1947. W. W. Wirth.

Allotype: ♀, Same data as holotype. Both specimens slide mounted. Types deposited in the United States National Museum.

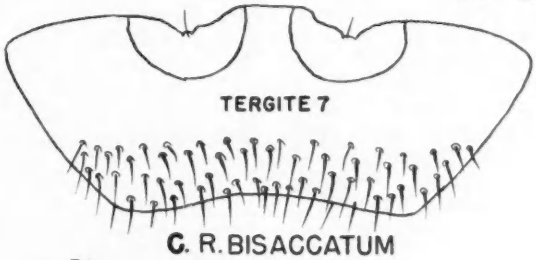
Rhegmoclemina (Neorhegmoclemina) bisaccatum, n. sp.

Male: Total length approximately 1.50 mm. Color dark grey brown, slightly shining; head jet black, shining; antennae dull black; a pale

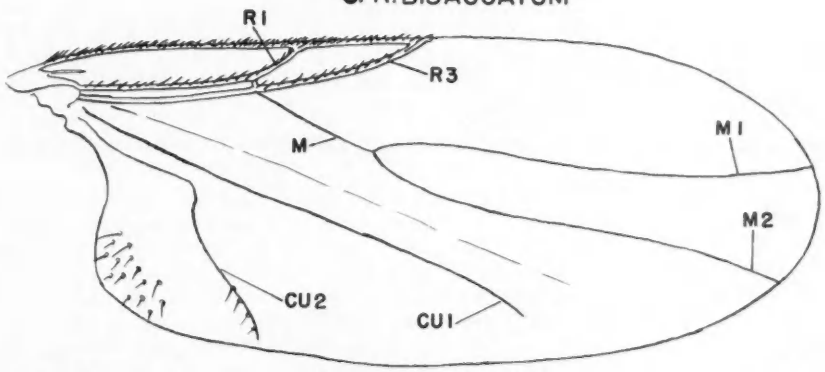


A. R. SCROBICOLLIS

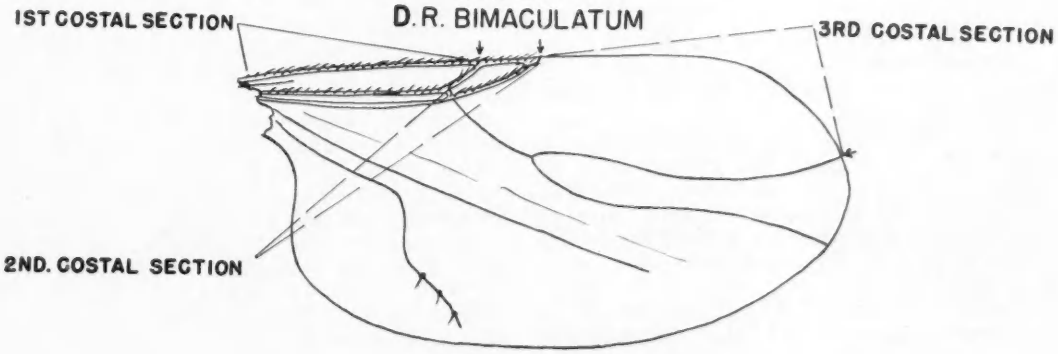
B. R. BISACCATUM



C. R. BISACCATUM



D. R. BIMACULATUM



E. R. ASYMMETRICUM

yellowish spot at each posterolateral corner of the scutum; abdomen grey brown, dull; legs grey brown, darker grey at apices of femora and bases of tibiae; halteres dark grey; empodia grey brown. Maxillary palpi short, 0.05 mm. long. Enlarged supra-alar setae in a definite row, 8 present; subspiracular setae 2.

Wings 1.30 mm. long; section 3 of costal margin 6.5 times as long as section 2; M_1 4.75 times as long as M; cell between M_1 and M_2 medially constricted as in Fig. 3E. A few macrosetae on Cu_2.

Segment 7 of abdomen as in Fig. 2G. It should be noted here, further, that an eighth tergite is also present. This is unique to this species. Genital vesica and apodemes 0.35 mm. long.

The male genitalia are not figured for this species, since they were accidentally destroyed during slide preparation of the only male of this species available. It was noted, however, that the genitalia are quite asymmetrical and resemble somewhat those of *R. parvum*.

Females: Total length 1.50 to 1.96 mm. Wing length 1.10 to 1.35 mm. (Holotype 1.27 mm.). Female genitalia (Fig. 3B) concolorous with abdomen. Supra-alar setae 15, the row double medially; subspiraculars 2. Tergite 7 bearing two sclerotized and darkly pigmented pockets on the anterior margin (Fig. 3C). These structures have not been seen in any other species in this genus. The female is otherwise identical with the male in color and chaetotaxy.

Since the single male of this species available is damaged, a female specimen has been chosen as the holotype, and no allotype will be designated until such time as additional males are available.

Holotype: ♀, Ames, Iowa, June 10, 1952, at window. W. L. Downs.

Paratypes: 1♂, Ames, Iowa, May 19, 1951, at window. W. L. Downs. 1♀, Ithaca, New York, July (no further data). All specimens slide mounted. Holotype deposited in the Iowa State College Collections.

Rhegmoclemina (Neorhegmoclemina) abruptinervis (Duda), new combination

Scatopse abruptinervis Duda, 1928. Konowia, 7: 279–280, Tafelfig. 2.

This species was described originally from a single male and a single female from Suiza de Turrialba, April 3, 1921 and May 1923. The types are in the Hungarian National Museum (*fide* Duda). The specimens at hand key to this species in Duda's key and agree in color and in wing venation.

Males: Total length 1.24 to 1.51 mm. Color dark brownish grey to black, dull; head jet black, dull; palpi yellowish grey to black; antennae dull black, basal segments brownish; abdomen dull brownish grey to black both dorsally and ventrally; legs lighter greyish brown, tarsi yellowish brown; halteres dark grey; empodia concolorous with tarsi. Maxillary palpi short, 0.068 mm. long. Supra-alar setae 5 to 7, in a definite row; a single subspiracular seta.

Wings 1.14 to 1.24 mm. long. Section 3 of the costal margin 6 times as long as section 2; M_1 slightly more than 2.5 times as long as M. No setae on Cu_2.

Segment 7 of the abdomen as in Fig. 2H. Tergite 7 sometimes longer and more acute. Genital vesica and apodemes 0.29 to 0.31 mm. long. Male genitalia as in Fig. 1D.

Females: Total length 1.38 to 1.45 mm. Wing length 1.21 to 1.24 mm. Female genitalia concolorous with abdomen. Supra-alar setae 8; subspiraculars 2. Otherwise identical with the male in color and chaetotaxy.

This species is similar to *R. parvum* in size and coloration. It differs, however, in the shape of tergite and sternite 7 and in wing venation. The two branches of M do not curve toward each other medially as in Fig. 3E but remain widely separated as in Fig. 3D. This species is also separated from all known species in this genus by the absence of setae on Cu_2.

Specimens examined: *Costa Rica:* 1♀, Suiza de Turrialba, August; 1♂, Higuito, San Mateo. *Panama C.Z.:* 1♂, 1♀, Summit, Dec. 1946; 1♀, Mojinga Swamp, Ft. Sherman, Dec. 1951; 1♂, Jan. 1953; 1♂, Loma Borracha, July, 1952; 1♂, Camaron, Ft. Kobbe, June 17, 1952; 1♀, Ft. Clayton, Sept. 22, 1951.

Rhegmoclemina (Neorhegmoclemina) asymmetricum, n. sp.

Male: Total length approximately 1.3 mm. Color dark greyish brown, dull; head black, dull; abdomen dull grey-brown; legs grey-brown, tarsi pale yellowish; setae pale brown; halteres dark grey. Maxillary palpi short, 0.035 mm. long. Enlarged supra-alar setae present in a definite row, 8 in number; a single large subspiracular seta present.

Wings (Fig. 3E) 1.03 mm. long. Section 3 of costal margin more than 6 times as long as section two. M_1 3.5 times as long as M. Setae present on Cu_2; Cu_2 gently curved.

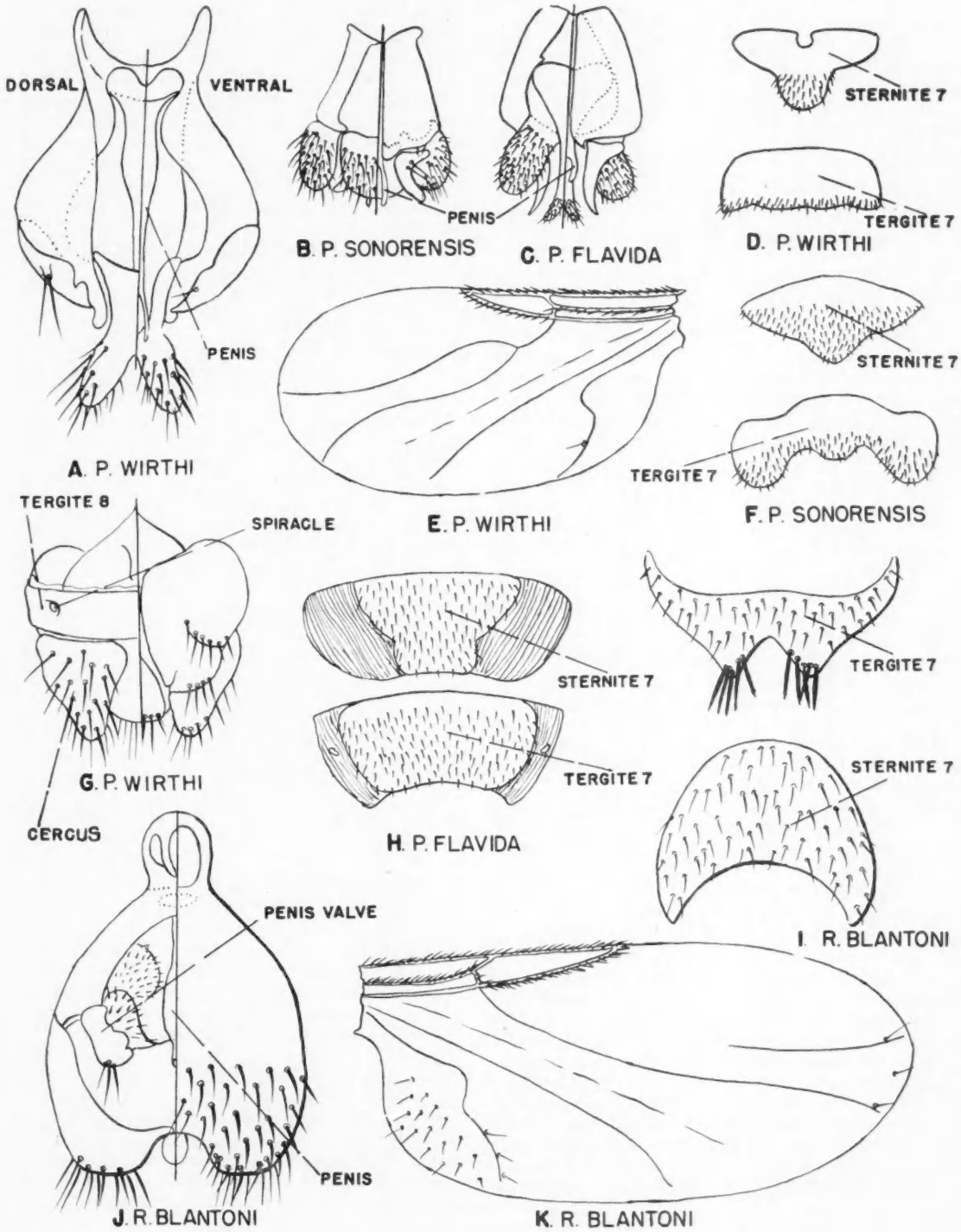
Segment 7 of the abdomen as in Fig. 2F. Male genitalia strikingly asymmetrical (Fig. 1G).

This species is closely related to *R. parvum* and *R. bisaccatum* as is shown by the form of the seventh sternite and the venation of the wings. It differs from both of these, however, in the structure of the male genitalia and smaller size.

Female: Unknown.

Holotype: ♂, Ocho Rios, Jamaica, Feb. 2, 1937. Chapin and Blackwelder.

Specimen slide mounted. Type in the collection of the United States National Museum.


DORSAL
VENTRAL
PENIS
A. P. WIRTHI
PENIS
B. P. SONORENSIS
C. P. FLAVIDA
STERNITE 7
TERGITE 7
D. P. WIRTHI
E. P. WIRTHI
STERNITE 7
TERGITE 7
F. P. SONORENSIS
TERGITE 8
SPIRACLE
CERCUS
G. P. WIRTHI
STERNITE 7
TERGITE 7
H. P. FLAVIDA
TERGITE 7
STERNITE 7
I. R. BLANTONI
PENIS VALVE
PENIS
J. R. BLANTONI
K. R. BLANTONI

Parascatopse, new genus

The species in this genus are all very small, ranging in size from 0.62 to 1.31 mm. The general coloration ranges from brown or grey-brown to black, and all are dull. One species has been found only in Florida, another in Florida and Mississippi and the third has been taken from several localities in the Imperial Valley in California.

Head: The head is hypognathous as in other genera in this family, slightly compressed laterally and only slightly elongate. The eyes are holoptic in both sexes and very finely pubescent. There are the usual three ocelli on the vertex. The antennae are ten- to twelve-segmented, at least as long as the head, of a dull black color, covered with a fine, silvery pubescence and a number of larger setae. The head capsule is convex behind the eyes and bears scattered, short, fine setae. A complete tentorium is present.

The mouthparts are reduced, the maxillary palpi are one-segmented, short, 0.034 mm. long, apically rounded, and covered with a fine pubescence and a number of larger setae. There is a sensory pit located at the apex of each maxillary palp. The labellae are small and palpiform, with no evidence of pseudotracheae and covered with pubescence and setae as are the maxillary palpi.

Thorax: The thorax is stoutly sclerotized but not particularly compressed laterally. The scutum and scutellum bear a number of short and rather fine setae which cover the whole surface. The setae are somewhat stouter and longer at the lateral margins of the scutum, but there is no regular row of supra-alar setae present. The sclerotized plate on which the anterior spiracle is located is smaller than in *Rhegmoclema* and is rounded rather than triangular. This sclerite bears a number of small setae surrounding the spiracle. There are no rows of stout setae anywhere on the pleural areas, only small scattered setae. There are two to four small subspiracular setae present beneath the posterior spiracle. The postnotal phragma is well developed as in other members of the family.

The wings (Fig. 4E) have the costa and radius and its remaining branches well sclerotized and pigmented; veins M and Cu are faint but visible. The costa and radius bear numerous macrosetae in all species. Vein Cu_2 bears a few macrosetae in all of the species known. There are no other macrosetae on the wings. The membrane is covered with microtrichia. Vein M_1 is complete in all species, and Cu_2 has two right-angled bends along its course giving the vein a Z-shape. The third section of the costal margin is from two to four times as long as the second, and vein M_1 is 2.5 to 5 times as long as vein M. The halteres are covered with microtrichia, and the capitulum bears a few small macrosetae, but the pedicel is bare. The capitulum is ovoid.

The tarsal segments are short but more slender than in *Rhegmoclema*. A lobe-like, marginally setaceous empodium is present, and the tarsal claws are small and simple. There are no conspicuous combs or spurs on the legs.

Abdomen: There are seven pregenital segments in the males and eight pregenital segments in the females. Each segment bears a pair of laterally located spiracles. Segment one is shorter than succeeding segments. Tergite two is a single sclerotized plate. There is no reticulate pattern developed in the cuticle of segment 1, nor are there any specialized setae developed on the posterior margin of sternite 6. The membrane of the abdomen is longitudinally ribbed as in other members of this family. The abdomen is rather sparsely covered with small fine setae. In the males the seventh sternite is posteriorly produced in a small median lobe (Fig. 4D, F and H).

Male genitalia: The male genitalia (Fig. 4A, B, C) are small and somewhat capsule-like, composed of the ninth segment and whatever vestigal parts of the succeeding segments that remain. Unlike the genitalia of *Rhegmoclema*, they are apparently not rotated but lie in their normal position with the morphologically dorsal side up. A pair of stoutly sclerotized, articulated structures occur on the ventral aspect of the ninth segment which may be the gonocoxites, termed here the gonoforceps. In two of the species there are in addition a pair of more laterally located, setaceous, articulated lobes (Fig. 4B, C). These are represented in the type species by sclerotized, posteriorly directed processes on the dorsal side of the ninth segment (Fig. 4A). There is in addition on the dorsal side a medial seta-bearing structure which is bifurcate in two species (Fig. 4A, C) and entire in the third (Fig. 4B). The penis is bifurcate in all species, although the bifurcation is confined to the apex only in the type species. These genitalia are quite distinctive from those already described for *Rhegmoclema*.

A "free" vesica is present in all of the species in this genus. This structure is relatively large in this group, ranging in size from 0.20 to 0.37 mm.

Female genitalia: The female genitalia do not offer any specific characters but they are quite distinctive from those of *Rhegmoclema* (Fig. 4G). Tergite 8 is entire and bears a pair of easily visible spiracles. Articulated posteriorly to tergite eight is a pair of apparent cerci. Segments 9 and 10 are represented by a small median lobe between the cerci. The female genitalia are much like those in *Rhegmoclemina* s.s. described elsewhere in this paper. There is a single well developed and sclerotized spermatheca in all species.

Type species of the genus is *Parascatopse wirthi* n. sp.

KEY TO THE SPECIES OF PARASCATOPSE

1. Antennae with 12 segments; tergite 6 of ♂ with a slight, setaceous, median lobe on the posterior margin; vein M_1 5 times longer than M. Very small species, 0.62 to 0.80 mm. . . . . **wirthi**
1a. Antennae 10-segmented; tergite 6 of ♂ without a setaceous median lobe; M_1 2.3 to 2.5 times longer than M. Larger species, 0.93 to 1.35 mm. 2
2. Yellowish brown species; macrosetae of antennae curved anteriorly; third section of costal margin 1.75 times as long as second. . . . . **flavida**
2a. Grey-brown species. Macrosetae of antennae straight; third section of costal margin 4.25 times as long as second. . . . . **sonorensis**

Parascatopse wirthi, n. sp.

Males: Total length 0.62 to 0.79 mm. Color dark brown, scarcely shining; head darker, somewhat infuscated; antennae dull black with a silvery pubescence; pleural areas of thorax shining; legs yellowish brown, lighter than thorax; scutum lighter at lateral margins; halteres light grey-brown. Antennae 12-segmented; macrosetae of antennae straight. Maxillary palpi short, 0.034 mm. long. No definite row of enlarged supra-alar setae; subspiracular setae 4 to 5.

Wings (Fig. 4E) 0.62 to 0.66 mm. long. Microtrichia longer than in species of *Rhegmoclema;* Cu_2 with two sharp right angled bends along its course, a single macroseta present; third section of costal margin 3.5 times as long as second; M_1 5 times as long as M.

Abdomen with few small scattered setae; tergite 6 with a slight, median, obtuse lobe bearing a cluster of long setae; segment 7 as in Fig. 4D; sternite 7 with a median obtuse lobe. Genital vesica and apodemes 0.20 mm. long. Male genitalia as in Fig. 4A.

Females: Total length 0.80 mm.; wing length 0.72 mm. Two macrosetae on Cu_2; subspiracular setae 2; no median, setaceous lobe on tergite 6; setae longer on tergite 7; tergite 8 with spiracles located dorsally. Female genitalia as in Fig. 4G. Otherwise identical in color and chaetotaxy with the males.

Holotype: ♂, Ft. Lauderdale, Florida, Aug. 13, 1951, W. W. Wirth. (Slide mount) Allotype: ♀, same data. (Slide mount).

Paratypes: 12♂♂, same data.

Holotype and allotype in the collections of the United States National Museum.

Parascatopse flavida, n. sp.

Males: Total length approximately 1.35 mm. (slide mounted). Color yellowish brown, not shining; head somewhat infuscated; pleural areas of thorax shining yellow-brown; legs yellowish, lighter than thorax; scutum paler at the margins; halteres sordid white; abdominal segments paler yellow brown on the posterior third; setae all pale yellowish to silvery. Macrosetae of the antennae curved toward the antennal apex; antennae with only 10 segments. Maxillary palpi short, 0.034 mm.; 4 subspiracular setae.

Wings 0.93 to 1.10 mm. long; Cu_2 with two sharp, right angled bends; Cu_2 with 2 macrosetae; third section of costal margin 1.75 times as long as second; M_1 2.3 times as long as M.

Each abdominal segment with a small number of short, fine setae; no lobes or seta clusters on tergite 6; segment 7 as in Fig. 4H; sternite 7 with a truncate posterior lobe. Genital vesica and apodemes 0.37 mm. long. Male genitalia as in Fig. 4C.

Females: Unknown.

Holotype: 1 ♂, Florida, from muck soil, emerged May, 1929, Washington, D. C.

Paratype: 1♂, Pass Christian, Mississippi, June 8, 1917, Aldrich. This specimen has the head missing. It is unfortunate that the type locality of this species cannot be more precisely fixed.

Parascatopse sonorensis, n. sp.

Males: Total length 0.93 to 1.13 mm. Color dark grey-brown, dull except pleura shining; head black, dull, mouthparts yellowish; antennae dull black with silvery setae; tarsi yellowish; tibiae yellowish basally, the remainder of the legs dark grey-brown; scutum uniformly dull, dark grey-brown; halteres light grey. Macrosetae of the antennae straight, small; antennae with 10 segments. Maxillary palpi short, 0.034 mm.; 3 subspiracular setae.

Wings 0.86 to 1.00 mm. long; Cu_2 with distal bend less angulate than proximal; Cu_2 with 1 macroseta; third section of costal margin 4.25 times as long as second; M_1 2.6 times as long as M.

Abdominal segments with a few short, scattered setae; tergite 6 with a broad but slight median lobe but no seta cluster; segment 7 as in Fig. 4F.

Genital vesica and apodemes 0.30 to 0.32 mm. long. Male genitalia as in Fig. 4B.

Females: Total length 0.93 to 1.20 mm. long; wing length 0.83 to 0.93 mm.; 1 to 4 macrosetae on Cu_2; 3 subspiracular setae; no lobe on tergite 6. Female genitalia indistinguishable from those of *P. wirthi.* Otherwise identical in color and chaetotaxy with the males.

Holotype: ♂, Palo Verde, Imperial Co., California, April 8, 1949, W. W. Wirth.

Allotype: ♀, same data.

These types slide mounts. In the collection of the United States National Museum.

Paratypes: 5♂♂, 2♀♀, same data as holotype. 3♂♂, 2♀♀, Westmorland, Imperial Co., California, April 6, 1949. W. W. Wirth. 1♂, 2♀♀, Hot Mineral, Imperial Co., California, April 30, 1952. J. N. Belkin.

A NEW SPECIES OF RHEGMOCLEMA

Rhegmoclema blantoni, n. sp.

Male: Total length 1.75 mm. Color generally brown; antennae dull black; head capsule yel-

lowish brown with black blotches underlying, somewhat shining; thorax golden brown; scutellum and legs yellow; halteres grey; supra-alar setae black; abdominal tergite 1 yellow brown, tergites 2 to 6 dull black, tergite 7 yellow brown with black apical setae; abdominal sternites yellow brown. Head, thorax and abdomen bearing numerous, short, stout setae. Supra-alar setae very stout, 4 in number but not in a regular row; subspiracular setae 10, 1 stout and 9 small; there are in addition 2 pair of laterally located, long, black setae on the scutellum. Antennae 12-segmented; maxillary palpi short, 0.068 mm.

All tibiae with stout spur-like setae apically; first tarsal segment of all legs with a multiple row of stout spur-like setae apically.

Wings (Fig. 4K) 1.38 mm. long; third section of costal margin 2.6 times as long as second; M_1 basally incomplete; M_1 and M_2 with but a single macroseta each, Cu_1 without macrosetae, Cu_2 with 3 macrosetae, the membrane behind Cu_2 with several macrosetae.

Tergite of abdominal segment 1 with a well developed reticulate pattern on the cuticle; sternite 6 with a row of 7 short, very stout setae on the posterior margin. Segment 7 of the abdomen as in Fig. 4I. Genital vesica and apodemes 0.31 mm. long. Male genitalia as in Fig. 4J.

Females: Unknown.

Holotype: ♂, Almirante, Panama, Boscas del Toro Pr., Jan. 1953. F. S. Blanton.

This species is the second in the genus recorded from Central America. It differs from the previously recorded species *R. caudata* (Duda) in size (*R. caudata* 1.1 mm. long), in color (*R. caudata* is black), in the relative lengths of the third and second segments of costal margin(in *R. caudata* this is 1.6 to 1), and apparently in the male genitalia. The latter point is rather difficult to ascertain, however, from Duda's sketches (1928).

This species is most readily separated from the North American species by the shape of tergite 7 (Fig. 4I) and the reduction in the number of macrosetae on veins M_1 and M_2.

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UNDESCRIBED SPECIES OF JAPANESE CRANE-FLIES[1] (DIPTERA: TIPULIDAE)

PART VIII

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The preceding part of this series of papers was published in the Annals of the Entomological Society of America, 43: 418–436, 1950. The species discussed at this time were taken in various parts of Honshu and Kyushu by several friends and colleagues to whom my sincere thanks are extended for the privilege of retaining the types of the novelties in my private collection of these flies. Materials from Kyushu were taken by Messrs. Issiki and Ito; from Honshu, by Messrs. Fukuhara, Haruta, Hasegawa, Inoue, and Ito.

Genus **Tanyptera** Latreille

Tanyptera brevipecten n. sp.

Size medium (wing, male, about 12 mm.); general coloration black, the basal abdominal segments extensively yellow; antennal flagellum with the unpaired branch relatively short; femora yellow, the tips very narrowly black; wings with vein R_1+_2 oblique to suberect; male hypopygium with the outer dististyle relatively large, narrowed gradually into an acute blackened spine.

Male.—Length, about 14–15 mm.; wing, 12–12.5 mm.; antenna, about 4.0–4.1 mm.

Frontal prolongation of head and palpi black. Antennal scape brownish black, pedicel and flagellum paler, brown to yellowish brown, the branches darker; longest branches nearly three times the segments, the outer unpaired one much shorter, less than the segment itself; first flagellar segment with a short simple branch, segments two to ten, inclusive, with paired basal branches; terminal segment simple.

Head black. Thorax black, the praescutum

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and scutum more polished; dorsopleural membrane obscure yellow. Halteres with stem dusky, knob yellow. Legs with the coxae black; trochanters obscure yellow; femora yellow, the tips very narrowly black; tibiae and basitarsi obscure yellow, the tips very narrowly darkened; remaining tarsal segments more uniformly dark brown. Wings (Fig. 1) with a weak brownish tinge, the prearcular and costal fields a little more yellowed; stigma oval, dark brown; a paler brown cloud over the anterior cord; veins brownish black. Venation: R_{1+2} oblique to suberect, cell Sc_2 small to very small; petiole of cell M_1 from one to one and one-half times m; basal section of vein M_4 relatively long, erect.

First abdominal tergite and base of second black; succeeding tergites yellow, with a broad conspicuous black central stripe, the outer segments uniformly black; basal sternites yellow. Male hypopygium with the posterior border of tergite very gently emarginate. Outer dististyle relatively large, narrowed gradually into an acute blackened spine; inner dististyle about two-thirds as long, more or less parallel-sided.

Habitat: Japan (Kyushu). *Holotype:* ♂, Naidaizin, altitude 700 meters, May 25, 1952 (Issiki-Ito). *Paratype:* ♂, Kunimidake, altitude 1200 meters May 24, 1952 (Issiki-Ito).

Tanyptera brevipecten is most nearly allied to species such as *T. angustistyla* Alexander and *T. perangusta* Alexander, both of which are smaller forms with the structure of the male hypopygium, particularly the outer dististyle, quite distinct.

Genus **Macgregoromyia** Alexander
Macgregoromyia syusiro n. sp.

General coloration dark plumbeous gray; antennae and legs brownish black; wings with the restricted ground yellow, most of the surface suffused with darker; stigma and narrow seams over the cord dark brown; abundant macrotrichia in outer cells of wing; vein R_{1+2} preserved; r-m very strongly arcuated basad; abdomen dark brown, the basal sternites dimidiate, brown, the apices broadly testaceous yellow; ovipositor with the cerci small and slender.

Female.—Length, about 9.5 mm.; wing, 11 mm.; antenna, about 2 mm.

Frontal prolongation of head dark gray, nasus distinct; palpi black. Antennae brownish black, the scape and pedicel a trifle paler, 12-segmented; flagellar segments not enlarged basally, the intermediate ones subequal to the verticils. Front and anterior vertex light gray, posterior vertex dark grayish brown; no vertical tubercle; anterior vertex broad, approximately seven or eight times the diameter of the scape.

Pronotum dark brown. Mesonotum almost uniformly dark plumbeous, the praescutum with vague indications of a darker median brown line on anterior half; scutellum, postnotum and pleura lighter gray; dorsopleural membrane restrictedly obscure yellow. Halteres brown, the knob dark brown. Legs with the coxae gray; trochanters brownish gray; remainder of legs dark brown to brownish black. Wings (Fig. 2) with the restricted ground yellow, most evident in cells C and Sc; most of remainder of surface infuscated, appearing as central streaks in cells R and M, most of cells Cu and Anals, and as broad seams to the veins beyond cord, involving the entire wing tip; stigma oval, dark brown, conspicuous, preceded and followed by extensive whitened areas; narrow darker brown seams at anterior cord, less evident but distinct on the posterior cord; veins dark brown, paler in the costal field. Abundant macrotrichia in centers of cells beyond cord (indicated in drawing by stippling), extending from cells R_2 to Cu, inclusive. Venation: R_s short, about one-half R_{2+3}, R_{1+2} preserved; r-m very strongly arcuated basad; petiole of cell M_1 nearly twice m; cell 1st M_2 relatively narrow, parallel-sided or virtually so; basal sections of veins M_{1+2} and M_{3+4} subequal.

Abdominal tergites chiefly dark brown, the sternites dimidiate, brown basally, the posterior parts broadly testaceous yellow, on the sixth and succeeding segments more uniformly darkened; cerci and hypovalvae fulvous horn color. Ovipositor with cerci small and weak but slender, pointed at tips.

Habitat: Japan (Kyushu). *Holotype:* ♀, Naidaizin, altitude 600 meters, May 23, 1952 (Issiki-Ito).

This interesting fly is named for Professor Syusiro Ito, distinguished student of the Japanese Diptera. Despite the aberrant characters of the strong retention of vein R_{1+2} and the presence of abundant macrotrichia in the wing cells, I am referring this fly to *Macgregoromyia*, from all other known species of which it differs in the two points indicated. The only other generic assignment possible would seem to be in the subgenus *Mitopeza* Edwards of the genus *Dolichopeza* Curtis, but here, too, the characters are quite discordant. The discovery of the male sex might throw some further light on this question.

Macgregoromyia itoi n. sp.

General coloration dark brown, the praescutum vaguely striped with darker; antennae short; legs brownish black, the femoral bases restrictedly brightened; wings grayish subhyaline, cells C and Sc brown; stigma and a narrow seam over the anterior cord darker brown; R_s short, transverse; cell 1st M_2 small, about as long as the petiole of cell M_1; male hypopygium with the margins of the lobes of the tergites slightly produced; inner dististyle with its posterior border strongly convex, the caplike apex produced backward; beak with a low chitinized flange on side.

Male.—Length, about 9 mm.; wing, 11.3 mm.; antenna, about 3.2 mm.

Frontal prolongation of head relatively short, about one-half the remainder, buffy above, including the distinct nasus, dark brown on sides; palpi with basal two segments black, the outer two brown. Antennae with scape and pedicel testaceous yellow, flagellum brownish black; segments elongate-cylindrical, with very poorly developed basal tubercles; verticils very short, less than the diameter of the segment at the point of their insertion. Head brownish black, sparsely pruinose, more heavily and conspicuously so on the anterior vertex; front light gray; anterior vertex broad, nearly six times the diameter of the scape; vertical tubercle lacking.

Pronotum brown, more pruinose laterally. Mesonotum chiefly dark brown, the praescutum with vague indications of stripes, the median one narrowly bordered by darker and divided by a similar capillary vitta; lateral praescutal borders pruinose; posterior sclerites of notum dark brown. Pleura chiefly brownish gray, the ventral propleura, sternopleurite and meron darker brown; dorsopleural membrane more buffy. Halteres elongate, stem yellow, clearer basally, knob brownish black. Legs with the coxae pale brown; trochanters yellow; remainder of legs brownish black, the femoral bases restrictedly yellow; claws long and slender, simple. Wings grayish subhyaline, cells C and Sc brown; stigma and a narrow seam over the anterior cord dark brown, posterior cord more narrowly darkened; outer radial field and wing margin vaguely infuscated; veins brownish black. Venation: R_s short, transverse, about one-half longer than the basal section of R_{4+5}; cell 1st M_2 small, about as long as the petiole of cell M_1.

Abdominal tergites black, sternites brownish yellow, their bases blackened; outer segments, including hypopygium, blackened. Male hypopygium with the tergite large, the lobes broad, their outer lateral margins slightly more produced, glabrous; remainder of lobes with dense erect setulae and scattered relatively small setae; median region of tergal notch farther produced into a semicircular blade. Outer dististyle darkened, about four times as long as broad, the tip obtuse. Inner dististyle with the posterior border strongly convex, the caplike apex produced backward, the beak longer, with a low chitinized flange back from the tip.

Habitat: Japan (Kyushu). *Holotype:* ♂, Udonno, altitude 200–250 meters, May 15, 1952 (Issiki-Ito).

I am pleased to name this interesting fly for Professor Syusiro Ito, student of the Japanese Diptera, particularly the Empididae and Trypetidae. The most nearly allied species is *Macgregoromyia shikokuana* Alexander, of Shikoku, Japan. As has been discussed elsewhere, the discovery of members of the genus in southern Japan came as a surprise, the hitherto described forms occurring in eastern and southeastern Asia, from the Philippines to the Malay Peninsula, as far west as Szechwan, China. The various species are readily told among themselves by the details of venation and structure of the male hypopygium.

Genus **Nephrotoma** Meigen
Nephrotoma akitae n. sp.

Size relatively large (wing about 15 mm.); general coloration yellow contrasted with polished black or blue-black areas, including three praescutal stripes; male antennae with the flagellar segments strongly incised; occipital brand very large, subquadrate in outline; scutellum testaceous yellow, mediotergite yellow, its posterior border narrowly darkened; abdominal tergites yellow with an almost entire median black stripe, segments seven to nine, inclusive, black; ovipositor with the cerci and hypovalvae short and subfleshy; male hypopygium with the beak of the inner dististyle very long; ninth sternite with a conspicuous median appendage that is clothed with long reddish setae; gonapophysis microscopically setuliferous.

Male.—Length, about 15 mm.; wing, 14.5 mm.; antenna, about 5 mm.

Female.—Length, about 16 mm.; wing, 15 mm.

Frontal prolongation of head yellow, the apex darkened medially above, including the nasus; basal segment of palpus dark brown, the second and third segments brownish yellow, terminal segment black. Antennae (male) relatively long, as shown by the measurements; scape brownish yellow, pedicel dark brown, flagellum black; flagellar segments strongly incised, the outer node of each segment larger than the basal one. In the female, antennae shorter, the flagellar segments very feebly incised. Head yellow; occipital brand very large, subquadrate in outline, its anterior border truncate or virtually so.

Pronotum light yellow medially, the propleura black. Mesonotal praescutum yellow with three polished blue-black stripes that are vaguely bordered by more velvety black, including the cephalic border of the median stripe and a larger spot opposite the anterior end of the lateral stripe, this not reaching the margin, median praescutal stripe reaching the suture behind; lateral ends of suture blackened, the color continued cephalad along the extreme lateral

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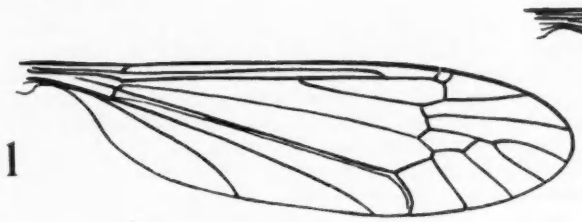
Explanation of Plate

Fig. 1. *Tanyptera brevipecten* n.sp.; venation.
Fig. 2. *Macgregoromyia syusiro* n.sp.; venation.
Fig. 3. *Nephrotoma akitae* n.sp.; male hypopygium.
Fig. 4. *Tipula* (*Indotipula*) *itoana* n. sp.; male hypopygium.
Fig. 5. *Tipula* (*Oreomyza*) *harutai* n. sp.; male hypopygium.
Fig. 6. *Tipula* (*Oreomyza*) *daitenjoensis* n.sp.; male hypopygium. (Symbols: *a*, aedeagus; *d*, dististyle; *g*, gonapophysis; *s*, sternite; *t*, tergite).



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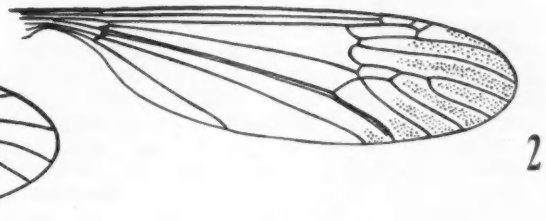

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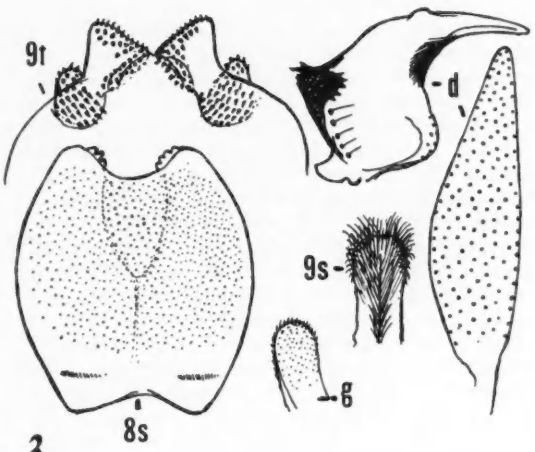

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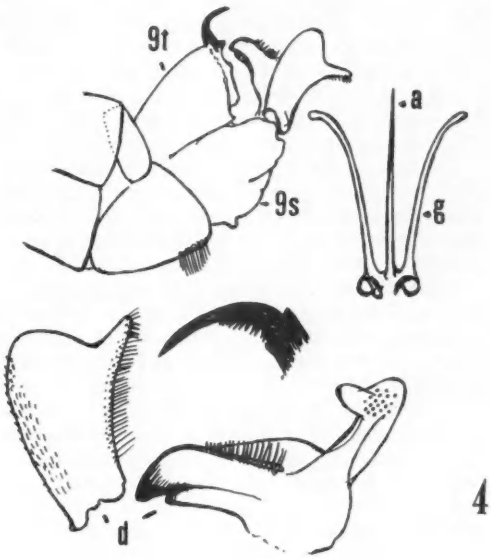

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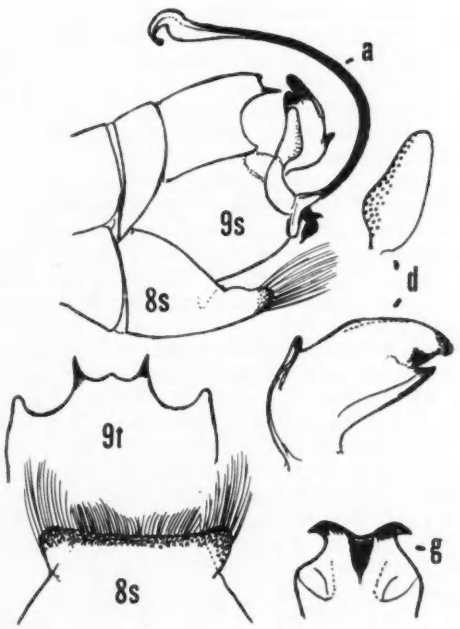

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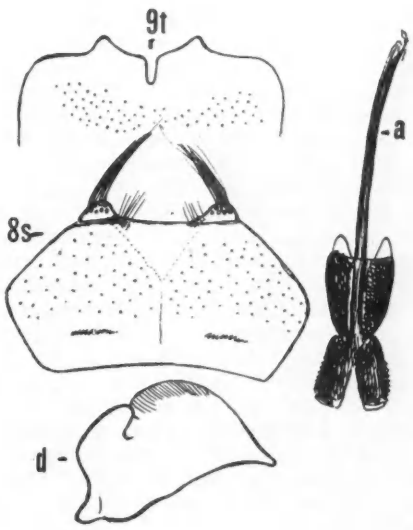

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border to nearly opposite the anterior end of the lateral stripe; centers of scutal lobes polished leaden black, the remainder of scutum yellow; scutellum testaceous yellow; mediotergite yellow, the posterior border narrowly darkened, pleurotergite dusky, the katapleurotergite extensively yellow. Pleura yellow, contrastedly patterned with black, including the ventral anepisternum, ventral sternopleurite, ventral meron and along the mesopleural suture; dorsopleural membrane extensively pale yellow. Halteres obscure brownish yellow. Legs with the coxae blackened basally, more extensively so on fore legs where more than the basal half is included, on the other coxae only the bases darkened, the setae abundant, pale; trochanters yellow; fore femora chiefly black, the basal two-fifths brownish yellow; remaining femora brownish yellow with approximately the outer sixth blackened; tibiae brown, the tips broadly black; tarsi black; claws apparently simple. Wings with the ground color yellowed, the prearcular and costal regions clearer; wing tip and anterior cord narrowly darkened; stigma oval, darker brown, with trichia. Venation: R_s oblique, fully twice the basal section of R_{4+5}; cell M_1 broadly sessile; m-cu at fork of vein M_4.

Abdominal tergites yellow with an only slightly broken mid-dorsal black stripe, interrupted at the cephalic borders of the individual segments; basal sternites yellow; segments seven to nine, inclusive, black. Ovipositor with the cerci short, somewhat as in *esakii;* hypovalvae with the terminal part very short, bent strongly ventrad. Male hypopygium (Fig. 3) with the ninth tergite, *9t*, transverse, narrowed outwardly, terminating in two triangular lobes, their apices obliquely truncated, densely spiculose; flange of ventral surface with unusually abundant spicules, jutting caudad on either side as a small lobe. Ninth sternite, *9s*, with a conspicuous median appendage, carinate beneath, densely provided with long reddish setae. Outer dististyle moderately long, its length about 3.5 times its greatest width. Inner dististyle, *d*, with the beak unusually long and slender, nearly straight; lower beak lacking; no dorsal crest but with a low rounded knob opposite the base of beak; posterior crest blackened and strongly armed with spinous points. Gonapophysis, *g*, shorter than the broad aedeagus, appearing as a slightly elongate blade, the surface microscopically setulose, apex rounded. Eighth sternite, *8s*, very large and sheathing, longer than broad, widest opposite midlength, thence narrowed, the posterior border produced into two low lobes, their ventral-mesal face with three or four tubercles, the lobes with dense relatively short yellow setae; median region for nearly one-half the length with shield-shaped membranous area that bears numerous strong setae.

Habitat: Japan (Honshu). *Holotype:* ♂, Yuze, Akita, altitude 250 meters, June 22, 1951 (Issiki-Ito). *Allotopotype:* ♀, pinned with the type.

In its general appearance the present fly is most like *Nephrotoma ozenumensis* Alexander, differing in all details of coloration, especially of the head and mesonotum. The hypopygial structure marks the present fly as very distinct.

Genus **Tipula** Linnaeus
Tipula (Indotipula) itoana n.sp.

General coloration of mesonotum orange, the pleura more whitened; head dark gray above, with a capillary dark brown line; wings brownish yellow, the prearcular and costal fields clearer yellow, stigma yellow; basal abdominal tergites yellow, the outer ones darker with narrow pale borders, sternites yellow; male hypopygium with the tergite produced medially into a pair of strong curved hooks, their mesal faces with abundant spines; outer dististyle a large broadly flattened blade that bears a slender lobe on outer margin; inner dististyle with its outer basal lobe elongate; aedeagus needle-like, the gonapophyses approximately as long and only a little stouter, their tips narrowly obtuse; eighth sternite with the posterior border scarcely emarginate, the midregion of the posterior border with a dense group of erect yellow setae.

Male.—Length, about 15–16 mm.; wing, 18.5–19 mm.; antenna, about 3.8–3.9 mm.

Female.—Length, about 23 mm.; wing, 20 mm.; antenna, about 3.8 mm.

Frontal prolongation of head yellow, relatively short, less than the remainder of head, nasus elongate; palpi brownish yellow, the terminal segment a trifle darker. Antennae relatively short, subequal in both sexes; scape and pedicel yellow, first flagellar segment brownish yellow, remaining segments dark brown, feebly incised in male, the longest verticils slightly exceeding the segments. Head above dark gray, with a capillary dark brown median vitta, the very short front and space surrounding the antennal fossae yellowed; no vertical tubercle; head beneath more ochreous.

Pronotum light reddish brown. Mesonotum chiefly orange, the lateral praescutal borders whitened, mediotergite more yellowed. Pleura and pleurotergite whitened. Halteres infuscated, the knob more heavily so, the base of stem narrowly yellowed. Legs with the coxae whitened; trochanters yellow; femora and tibiae obscure yellow, narrowly infuscated at tips; tarsi dark brown; spur-formula 0–1–2; claws (male) bidentate, the outer spine longer and more conspicuous than the basal one. Wings brownish yellow, the prearcular and costal fields clearer yellow; cell Sc deeper yellow; stigma yellow, its outer end narrowly more darkened; veins brown, more brownish yellow in the more brightened

fields. No squamal setae; trichia of outer medial veins sparse, virtually restricted to outer half of vein M_1; vein R_{4+5} with abundant trichia, more crowded outwardly. Venation: R_s about one-third longer than r-m; cell 1st M_2 long-pentagonal, m and petiole of cell M_1 subequal; m-cu on M_4 just beyond origin; cell 2nd A relatively narrow.

Basal abdominal tergite yellowed, the posterior half of the second and the succeeding ones darker, the borders narrowly and inconspicuously pale, the lateral margins becoming broader on the outer segments; sternites yellow; hypopygium, including the large outer dististyle, brownish yellow. Ovipositor with the cerci straight, slender; hypovalvae long, appearing as compressed blades. Male hypopygium (Fig. 4) with the suture separating the ninth tergite and sternite complete except at cephalic end. Ninth tergite, *9t*, terminating in two powerful blackened hooks that are directed dorsad and slightly caudad, the outer half or less slightly decurved; mesal faces of the hooks with a group of erect black spinous setae; base of hooks on either side produced into a low shoulder. Ninth sternite with a small median knob or tubercle. Outer dististyle, *d*, a large broadly flattened blade, the lower apical region farther produced into a slender lobe that is fringed along margin with dense erect setae, near outer end of the expanded blade with an extensive whitened area. Inner dististyle, *d*, with the beak stout, lower beak obtusely rounded at tip; outer basal lobe a strong outwardly directed arm, at apex more expanded, as shown; region of the dorsal crest bearing a row of about 20 strong bristles, the longest being at the inner end of the row, becoming progressively shorter outwardly. Phallosome consisting of the long very slender acicular aedeagus, *a*, and the almost as slender subtending apophyses, *g*, the tips of the latter narrowly obtuse. Eighth sternite, *8s*, only moderately sheathing, the posterior border scarcely emarginate; immediately back from the border, the midregion with a dense group of erect yellow setae.

Habitat: Japan (Honshu). *Holotype:* ♂, Yatsugatake, Shinano, altitude 1250 meters, August 9, 1949 (Ito). *Allotopotype:* ♀. *Paratopotype:* ♂.

This is another of the interesting novelties discovered by Professor Syusiro Ito and which I am pleased to name in his honor. The nearest ally is *Tipula* (*Indotipula*) *yamata* Alexander, in which the male hypopygium is entirely distinct in structure.

Tipula (Oreomyza) harutai n.sp.

Allied to *yusou;* general coloration gray, the praescutum with four slightly more infuscated stripes that are bordered by dark brown; no nasus; basal two antennal segments yellow, the scape narrowly darkened at base, flagellum black, the segments rather strongly incised; femora obscure yellow, the tips black; wings whitened, the base and costal region more yellowed; a conspicuous clouded pale brownish gray pattern with darker areas at stigma, anterior cord and over the bases of cells R and M; basal abdominal segments yellow, the outer ones blackened; male hypopygium large and conspicuous; ninth tergite with the median region of posterior border produced into a plate, each lateral angle extended into a sharp spine; aedeagus very large and conspicuous, blackened; eighth sternite with the posterior border truncate, the lateral angles produced into conspicuous lobes, the entire border with long yellow setae.

Male.—Length, about 13–14 mm.; wing, 16–17 mm.; antenna, about 5 mm.

Frontal prolongation of head brownish black, pruinose at base, without nasus; palpi black. Antennae with scape obscure yellow, more or less darkened at base; pedicel yellow; flagellum black, the segments rather strongly incised, somewhat more strongly so in the paratype; segments about equal in length to the longest verticils. Head gray, darker on the genae; vertical tubercle conspicuous, weakly biolobed.

Pronotum gray, darkened medially. Mesonotal praescutum brownish gray, with four slightly more infuscated stripes that are narrowly margined with dark brown, the anterior ends of the borders of the intermediate stripes becoming obsolete in front, the outer borders of the lateral pair similarly obliterated behind; central dark stripe very conspicuous; posterior sclerites of notum gray, the scutal lobes each with two brown areas; katapleurotergite light gray. Pleura dark gray, variegated with paler gray across the dorsal sternopleurite and lower pteropleurite. Halteres pale, the base of knob a trifle darker. Legs with the coxae light gray; trochanters obscure yellow; femora obscure yellow, the tips rather broadly and conspicuously blackened, the amount subequal on all legs; tibiae black, a trifle more brightened basally; tarsi black; claws (male) toothed. Wings with the ground color whitened, the prearcular and costal fields light yellow; a conspicuous clouded pale brownish gray pattern, most evident in the outer and posterior cells, basad of cord appearing as longitudinal areas in the centers of cells R and M; stigma and a confluent seam over the anterior cord dark brown; a small but conspicuous dark brown postarcular area in cells R and M; both ends of cell 2nd A conspicuously whitened; veins dark brown, yellow in the flavous areas. Venation: R_s and R_3 subequal; cell 1st M_2 small, pentagonal in outline; petiole of cell M_1 a trifle longer than m; m-cu close to fork of M.

Abdomen with basal tergites obscure yellow, with a vague brown sublateral stripe, most

distinct at base; outer four segments uniformly brownish black. Male hypopygium (Fig. 5) large and conspicuous; basistyle entire. Ninth tergite, *9t*, with the median area produced into a transverse plate, each lateral angle of which is produced into an acute spine, the median area with a low triangular point; median plate separated from the sides by a broad U-shaped notch. Ninth sternite produced into a small slender lobe on either side of the phallosome. Outer dististyle, *d*, unusually short and stout, broadest on basal half, narrowed to the obtuse tip, the entire posterior border fringed with very long setae. Inner dististyle, *d*, with both beaks blackened; a very low and inconspicuous dorsal crest; outer basal lobe a small blackened spinous point, its tip obtuse. Gonapophysis, *g*, with the lateral blackened points unusually small, directed laterad, the decurved median point longer, its tip suddenly narrowed to an acute point. Aedeagus, *a*, very large and conspicuous, blackened, the tip paler, decurved. Eighth sternite, *8s*, sheathing, the entire posterior border truncate, each lateral angle produced into a stout lobe that is provided with a brush of long yellow setae, the transverse median part with shorter setae, these angularly bent at near mid-length.

Habitat: Japan (Honshu). *Holotype:* ♂, Mount Takao, May 5, 1950 (Haruta). *Paratopotype:* ♂, May 13, 1950 (Inoue).

The species is named for Mr. Toshiro Haruta. The fly is readily told from other members of the *yusou* group by the wing pattern and, especially, the structure of the male hypopygium, including the tergite, gonapophysis, and eighth sternite. The most similar species is *Tipula* (*Oreomyza*) *subyusou* Alexander, with which the present fly was associated in nature.

Tipula (Oreomyza) daitenjoensis n.sp.

General coloration light gray, the praescutum with three darker stripes; nasus lacking; antennae short, black throughout; legs black, the femoral bases obscure yellow; wings weakly brownish with a restricted darker brown pattern and more extensive whitened areas, including cells M, Cu and a poststigmal band; basal tergites yellow, trivittate with dark brown, outer segments more uniformly blackened; male hypopygium with the posterior margin of the ninth tergite smooth, with a small narrow U-shaped notch; inner dististyle entirely blackened, its outer basal lobe a large darkened appendage; eighth sternite large, the posterior border membranous, on either side with a low hemispherical lobe that bears a pencil of setae.

Male.—Length, about 18 mm.; wing, 18 mm.; antenna, about 4 mm.

Frontal prolongation of head elongate, a little shorter than the remainder, light gray above, dark brown on sides and beneath; nasus lacking; palpi brownish black. Antennae (male) relatively short, as shown by the measurements, black throughout, the scape slightly pruinose; flagellar segments with basal enlargements small and inconspicuous, the segments a little longer than the longest verticils. Head light gray, washed with pale brown across the posterior vertex and behind the eyes, the orbits narrowly gray; vertical tubercle very low, impressed medially.

Pronotum brownish gray, the scutellum lighter gray. Mesonotal praescutum light gray with three stripes, the broad median one dark gray, paler behind, narrowly bordered by brown along the interspaces, the cephalic third with a vague median darkening; lateral stripes small, paler brown; posterior interspaces slightly infuscated; posterior sclerites of notum clear light gray, the scutal lobes each with two separate brown areas; scutellum and mediotergite with vague indications of a capillary central darkening. Pleura clear light gray, the dorsopleural membrane medium brown. Halteres with stem yellow, knob dark brown. Legs with all coxae clear light gray; trochanters brownish gray; femora black, the bases rather narrowly obscure yellow, narrowest on the fore pair where about the proximal fifth is involved, on the posterior legs including slightly more than the basal fourth; remainder of legs black; claws (male) small, with a basal tooth. Wings with the ground brownish, conspicuously patterned with whitened areas, including a band beyond the stigma that extends to cell 1st M_2; two major areas in cell M, the outer one passing into cell *Cu;* a further major white area at near midlength of cell 1st A; more restricted whitenings at axilla and in bases of cells 1st M_2 and M_3; restricted darker marks include the stigma and a confluent seam over the anterior cord and a very small mark at origin of R_s; veins brown, the obliterative areas whitened. Venation: R_s long, exceeding two and one-half times m-cu; R_{1+2} entire but short and oblique; cell M_1 very deep, its petiole less than one-half m.

Abdomen with the basal tergite clear gray; tergites two to four yellow, the lateral borders broadly light gray, margined internally by a dark brown stripe that is almost continuous; a central black stripe, narrowly interrupted at the posterior margins of the segments; fifth and succeeding segments more uniformly blackened, more or less pruinose; basal sternite gray, segments two to four yellow, remaining segments darkened. Male hypopygium (Fig. 6) with the ninth tergite, *9t*, transverse, its posterior border with two broad subtruncated lobes, separated by a small and narrow U-shaped notch. Outer dististyle not clearly apparent in the type slide. Inner dististyle, *d*, entirely blackened, compact, the beak small and slender; dorsal crest strongly ribbed; outer basal lobe a

large darkened appendage. Phallosome represented by a small blackened cylinder or collar, with the aedeagus, *a*, jutting through it. Eighth sternite *8s*, narrowed outwardly, the median region of the apex filled with pale membrane; on either side of the posterior border with a low hemispherical lobe that bears a pencil of setae, directed slightly inward but not decussate.

Habitat: Japan (Honshu). *Holotype:* ♂, Mount Daitenjo, Shinano, altitude 2900 meters, July 26, 1951 (Inoue).

In the lack of a nasus, the present fly appears to fall in the group of flies that center about *Tipula* (*Oreomyza*) *yusou* Alexander and allies, differing evidently in the coloration and structure of the antennae and male hypopygium. The resemblance to species such as *T.* (*O.*) *matsumuriana* Alexander and *T.* (*O.*) *trupheoneura* Alexander seems more superficial.

Genus **Limonia** Meigen
Limonia (**Geranomyia**) **hakoneana** n.sp.

General coloration of mesonotum brownish gray, the praescutum with three narrow more blackened stripes; rostrum long, black; head above grayish brown with a central gray vitta; ventral thoracic pleurites light yellow; halteres yellow, the apex of knob slightly darkened; legs brownish yellow, unpatterned; wings tinged with yellow, with a sparse but evident brown pattern, including spots at various points and with narrow seams over the cord and outer end of cell 1st M_2; Sc long, Sc_1 ending about opposite three-fourths R_s, Sc_2 near its tip; abdomen dark brown, the posterior borders of the tergites narrowly yellow; male hypopygium yellow, rostral spines two, relatively short, straight.

Male.—Length, excluding rostrum, about 6.5 mm.; wing, 7 mm.; rostrum, about 3 mm.

Rostrum intensely black, nearly one-half the body; palpi black. Antennae black throughout, short; flagellar segments oval, the terminal one about one-half longer than the penultimate; verticils subequal to the segments. Head above grayish brown, with a central gray vitta, involving the front and a slightly broader line over the vertex.

Pronotum obscure yellow, narrowly darker laterally. Mesonotal praescutum narrowly yellowed in front, more brownish gray behind, with three narrow more blackened stripes, the lateral pair far removed from the margin; posterior sclerites of notum brownish gray, the scutal lobes with darker centers. Pleura brownish testaceous above, paling to light yellow on the sternopleurite and meron. Halteres pale yellow, the apex of knob slightly darkened. Legs with the coxae and trochanters light yellow; remainder of legs brownish yellow, unpatterned, the outer tarsal segments a trifle darker; claws with an outer major spine and two or three smaller more basal denticles. Wings tinged with yellow, slightly more saturated in the prearcular and costal fields; a very restricted but clear-cut brown pattern, including small spots at h, anterior arculus, supernumerary crossvein in cell Sc, origin of R_s, fork of Sc and as marginal clouds at ends of the longitudinal veins, those at R_{4+5} and M_{1+2} confluent; narrow but conspicuous seams at cord and outer end of cell 1st M_2; stigma brown, conspicuous, its center paler; veins yellow, darker in the patterned areas. Venation: Sc long, Sc_1 ending about opposite three-fourths R_s, Sc_2 near its tip; cell 1st M_2 longer than vein M_{1+2} beyond it; m-cu at fork of M.

Abdominal tergites dark brown, the posterior borders narrowly yellow; hypopygium yellowed. Unfortunately, the male hypopygium was lost before mounting on a slide; two straight rostral spines of moderate length were present, about as in *gifuensis*.

Habitat: Japan (Honshu). *Holotype:* ♂, Miyanoshita, Hakone, August 31, 1950 (Collector unknown).

The present fly is readily told from other regional species having patterned wings by the reduced pattern, with a different arrangement of the markings, and by the structure of the male hypopygium. Such forms with patterned wings include *Limonia* (*Geranomyia*) *avocetta* (Alexander), *L.* (*G.*) *multipuncta* (Alexander), and *L.* (*G.*) *radialis* Alexander; *L.* (*G.*) *gifuensis* (Alexander), with a somewhat similar hypopygium, has the wings unpatterned.

Genus **Dicranoptycha** Osten Sacken
Dicranoptycha hasegawai n.sp.

Generally similar to *edashigeana;* mesonotum polished fulvous yellow, with four polished black areas; legs yellow, the tips of the femora and bases and tips of the tibiae abruptly black; wings tinged with brown, darker along the costal border; abdomen, including hypopygium, black; male hypopygium with the phallosome unusually small, the gonapophyses appearing as short straight yellow spines.

Male.—Length, about 9 mm.; wing, 9 mm.

Female.—Length, about 9 mm.; wing 10 mm.

Rostrum obscure brownish yellow; palpi obscure yellow basally, the outer two segments black, the terminal one enlarged. Antennae obscure yellow, the outer segments darker. Head dark brown, paler on occiput and beneath.

Thorax polished fulvous yellow, the praescutum in cases with a pair of more reddish intermediate stripes, these obsolete in the type, better indicated in the allotype; a pair of large black areas on sides of praescutum with a second pair on the scutal lobes. Halteres weakly darkened, the knobs slightly more so. Legs with the coxae and trochanters yellow; femora yellow, the tips

abruptly and conspicuously black, the amount subequal on all legs and including about the outer tenth; tibiae yellow, the bases narrowly blackened, a little less than the femoral tips, the apices similarly blackened; basitarsi yellow, narrowly darkened at tip; outer tarsal segments passing into brownish black. Legs more slender and less conspicuously hairy than in *edashigeana*. Wings with a brownish tinge, still darker along the costal border to the apex, the extreme base more yellowed; conspicuous white lines in cell R adjoining vein M, behind basal half of vein 1st A, and the usual fork in cell Cu; veins brown. Venation: Cell 1st M_2 relatively small, about two-thirds vein M_4; m-cu about one-third its length beyond fork of M.

Abdomen, including hypopygium, black. Male hypopygium with the posterior border of the ninth tergite weakly biolobed. Outer dististyle slender, narrowed to a long gently curved terminal spine, the surface before the point with very weak microscopic spinulae; inner dististyle dusky, pointed at tip. Phallosome unusually small for a member of the group, the central area terminating in two low blunt lobes that are separated by a broad U-shaped notch. Each gonopophysis appearing as a short straight yellow spine.

Habitat: Japan (Honshu). *Holotype:* ♂, Mount Norikura, near Reisen-goya, Shinano, altitude 2400 meters, September 8, 1951 (Hasegawa). *Allotopotype:* ♂, September 7, 1951.

I am pleased to name this interesting fly for the collector, Mr. H. Hasegawa, student of the Japanese Hemiptera, to whom I am indebted for many crane-flies from the Japanese Alps. The species is most similar to *Dicranoptycha edashigeana* Alexander, of Shikoku, which differs in details of coloration, the stouter and hairier legs, and especially the structure of the male hypopygium, particularly the phallosome.

Genus **Dicranota** Zetterstedt

Dicranota (Rhaphidolabis) paraconsors n.sp.

Allied to *consors;* general coloration of thorax ochreous; head light gray; antennae short, 13-segmented, dark brown, the scape yellow; wings very pale yellow, unpatterned, veins pale; R_{2+3+4} longer than R_2; abdominal tergites brown, the subterminal segments darker to form a ring; male hypopygium with the posterior border of tergite almost truncate, the lateral arms slender; interbase distinctive, at apex produced into a gently curved spine.

Male.—Length, about 5.5 mm.; wing, 6 mm.

Rostrum yellow; palpi obscure yellow. Antennae 13-segmented, relatively short, only a little longer than the head; scape yellow, the remainder dark brown; flagellar segments oval to long-oval. Head light gray.

Thorax ochreous, the praescutum a trifle darker brown, especially medially; posterior sclerites and the pleura clearer yellow. Halteres with stem whitened, the knob infuscated. Legs with the coxae and trochanters yellow; femora brown, the remainder somewhat paler brown, only the outer tarsal segments darkened. Wings very pale yellow, unpatterned, the veins before the cord only a little darker than the ground, more infuscated beyond the cord. Venation: R_{2+3+4} longer than vein R_2; cell M_1 present; m-cu nearly its own length beyond the fork of M.

Abdominal tergites brown, the subterminal segments still darker to form a subterminal ring; basal sternites more yellowed. Male hypopygium with the tergite large, its posterior border nearly truncate to very feebly and gently convex, with relatively sparse stout marginal setae; lateral tergal arms appearing as strong simple horns or slender blades. Basistyle with the outer apical angle produced into a stout lobe, the outer half with numerous spinous setae; inner apical angle only slightly produced, with short setae; mesal face of style with a group of about ten long powerful setae, as in *consors* and allies. Interbase a strongly built structure, at apex produced into a gently curved spine, inner margin of dilated part of blade microscopically serrulate, somewhat as in *neoconsors*. Dististyle subequal in length and general size to the outer lobe of the basistyle, appearing as a flattened mittenlike blade, the apex obtuse; basal half with abundant delicate setae from conspicuous tubercles.

Habitat: Japan (Honshu). *Holotype:* ♂, Yatsugatake, Shinano, altitude 2000 meters, August 10, 1949 (Ito).

The structure of the male hypopygium readily distinguishes the present fly from other members of the *consors* group, particularly the ninth tergite and the interbase. It is closer to *Dicranota* (*Rhaphidolabis*) *consors* Alexander and *D.* (*R.*) *neoconsors* Alexander than to the very different *D.* (*R.*) *subconsors* Alexander.

Genus **Cladura** Osten Sacken

Cladura (Cladura) fuscivena n.sp.

Size small (wing, female, 7 mm.); general coloration of mesonotal praescutum gray with a broad central darker stripe that is more blackened in front; posterior sclerites of notum extensively yellow, pleura chiefly dark brown; halteres yellow; femora yellow, the tips gradually dark brown, on the fore pair including about the outer fifth, less extensive on the other legs; wings whitish subhyaline, restrictedly patterned with brown; a supernumerary crossvein in cell R_3; abdomen dark brown.

Female.—Length, about 6 mm.; wing, 7 mm.

Rostrum dark gray; palpi black. Antennae 14-segmented, the fusion-segment apparently involving three segments; scape reddish brown, remainder of organ black. Head dark gray.

Pronotal scutum brown, scutellum yellow. Mesonotal praescutum gray with a broad central darker stripe that is more blackened in front, scutal lobes similarly darkened; region of suture, central area of scutum, lateral margins of scutellum and parascutella more yellowed; postnotum brownish yellow, the cephalic part somewhat clearer yellow. Pleura chiefly dark brown, the metapleura more yellowed. Halteres yellow. Legs with the coxae and trochanters yellow; femora yellow, the tips gradually dark brown, somewhat more extensive on the fore legs where about the outer fifth is included, on the posterior femora involving about the outer seventh; tibiae yellow, the tips narrowly blackened; tarsi black, the proximal ends of the basitarsi a little paler. Wings whitish subhyaline, the prearcular and costal fields slightly more yellowed; a restricted but conspicuous brown pattern, most evident at origin of R_s, cord, fork of Sc, supernumerary crossvein in cell R_3 and as a seam along vein Cu; a clearer more yellowish white stigmal area beyond the fork of Sc; veins brown, darker in the patterned area, clear yellow in the flavous portions. Venation: Sc_2 subequal to Sc_1; R_2 far distad, at outer end of the pale stigmal area, more or less in alignment with the supernumerary crossvein in cell R_3; petiole of cell M_1 shorter than m; m-cu at near midlength of M_{3+4}.

Abdomen dark brown, the pleural membrane pale. Genital segment yellow; valves of ovipositor slender, including the cerci.

Habitat: Japan (Honshu). *Holotype:* ♀, Sugadaira, Shinano, October 16, 1950 (Hasegawa).

Most similar to the larger and more blackened *Cladura* (*Cladura*) *machidella* Alexander, differing in all details of coloration. As is the case in the latter fly, it remains questionable as to whether the crossvein in cell R_3 of the wings is adventitious or supernumerary in nature.

Cladura (Cladura) bicornuta n.sp.

Belongs to the *megacauda* group; general coloration yellow, the mesonotal praescutum and scutal lobes more reddened; legs yellow, the femoral tips narrowly and gradually infuscated, tarsi brownish black; wings pale yellowish subhyaline, unpatterned; male hypopygium with the posterior border of tergite produced into two obtuse lobes that are separated by a U-shaped notch, the sides of the tergite further produced into slender curved horns; outer lobe of basistyle shorter than the dististyle, the latter densely spiculose at apex; gonapophysis with more than the apical half dilated into a flattened glabrous blade; aedeagus small and slender.

Male.—Length, about 6–7 mm.; wing, 7.5–8.5 mm.

Female.—Length, about 8 mm.; wing, 10 mm.

Rostrum and palpi yellow. Antennae obscure yellow, the outer flagellar segments darker. Head brownish gray.

Thorax almost uniformly yellow, the mesonotal praescutum and the scutal lobes more reddened. Halteres yellow. Legs yellow, the femoral tips narrowly and gradually infuscated; tarsi brownish black. Wings pale yellowish subhyaline, the prearcular and costal fields deeper yellow; veins brown, paler in the brightened areas. Venation: R_{2+3+4} and R_{2+3} subequal; R_2 pale, placed in the whitened stigmal area; petiole of cell M_1 longer than m.

Abdomen pale brown, the extreme posterior borders of the segments paler. Male hypopygium with the ninth tergite distinctive, the posterior border with two obtuse lobes that are separated by a U-shaped notch, the sides of the tergite farther produced into slender curved horns; tergite just laterad of the intermediate lobes with about six or seven long setae. Basistyle with a small curved hairy lobe on mesal face before midlength; a larger lobe at extreme base of mesal face of style, provided with long conspicuous setae at base, narrowed outwardly into a subacute point; outer lobe of style shorter than the dististyle, slightly dilated outwardly, provided with long yellow setae. Dististyle slender, at apex bent or deflected at nearly a right angle, the tip with very dense microscopic points to produce a macelike appearance. Gonapophysis with more than the apical half dilated into a large flattened glabrous blade. Aedeagus small and slender, extending caudad to shortly beyond the apophyses.

Habitat: Japan (Honshu). *Holotype:* ♂, Sirahone-onsen, Shinano, altitude 1500 meters, September 9, 1951 (Hasegawa). *Allotype:* ♀, Mount Norikura, Shinano, near Reisen-goya, altitude 2400 meters, September 8, 1951 (Hasegawa). *Paratypes:* 3, with the allotype.

Most similar to *Cladura* (*Cladura*) *megacauda* Alexander, differing in the structure of the male hypopygium, especially the tergite, basistyle and phallosome.

Cladura (Cladura) telephallus n.sp.

Belongs to the *megacauda* group; size small (wing, male, 6.5 mm.); general coloration of entire body yellow; male hypopygium very large, the tergite narrowed into a depressed-flattened plate that divides at apex into two obtuse lobes; gonapophysis short-stemmed, the apex dilated into a large blade; aedeagus very long and extended, terminating in an acute spinous point.

Male.—Length, about 5 mm.; wing, 6.5 mm.

Rostrum and palpi yellow. Antennae and head pale yellow.

Thorax uniformly pale yellow. Halteres yellow. Legs yellow, the tips of the femora narrowly and abruptly blackened, of the tibiae less evidently so; tarsi passing into brown. Wings subhyaline; veins pale brown. Venation: Petiole of cell M_1 at least twice as long as m, in cases longer.

Abdomen yellow, relatively short, the unusually large and conspicuous male hypopygium approximately one-third the total length; hypopygium reddish yellow, the ventral part of the ninth sternite conspicuously blackened. Male hypopygium with the tergite narrowed outwardly into a depressed-flattened plate that is divided at apex into two obtuse lobes that are separated by a very narrow median split; no lateral tergal arms or projections. Basistyle elongate, with a conspicuous appressed lobe on mesal face at base, this provided with scattered spinous setae and close-set abundant microscopic spiculose points; apical lobe of style shorter than the dististyle, stout, with long conspicuous setae on outer third. Dististyle narrowed on outer third, the apex obtuse, flattened, with a very few long setae but without spicules, as in some related forms. Gonapophysis short-stemmed, the apex broadly dilated into an oval flattened blade. Aedeagus unusually long and extended, in a position of rest directed caudad and ventrad and finally cephalad, the terminal third a slender acute spinous point.

Habitat: Japan (Honshu). *Holotype:* ♂, Oze, Hatomati Toge, Kotsuke, September 22, 1950 (Hasegawa). *Paratopotypes:* 2 ♂♂.

The present fly is entirely distinct from other members of the ***megacauda*** group in the structure of the male hypopygium, especially the tergite, basistyle and aedeagus. The latter organ is somewhat noteworthy and contrasts markedly with the condition in some other members of the group where it is very small and inconspicuous.

Genus **Teucholabis** Osten Sacken
Teucholabis (**Paratropesa**) **inouei** n.sp.

Head black; mesonotum black, only the humeral region of the praescutum restrictedly reddened; pleura chiefly blackened; femora black, the bases yellow; posterior tibia (male) conspicuously dilated at apex; wings whitened, patterned with dark brown, including a band over the cord and the slightly wider wing tip; abdomen black, the posterior borders of the intermediate segments restrictedly pale; male hypopygium with the apex of the basistyle obtuse; inner dististyle complex.

Male.—Length, about 9 mm.; wing, 9 mm.

Rostrum, palpi and antennae black; flagellar segments oval, becoming more elongate outwardly, shorter than the verticils. Head dull black.

Pronotum narrowly dark brown medially, reddish yellow on sides. Mesonotum black, the humeral region of praescutum restrictedly reddened; pleurotergite black. Propleura orange; mesopleura chiefly black, the dorsal sternopleurite and metapleura restrictedly orange. Halteres with stem brownish black, knob darkened, with the apex obscure yellow. Legs with all coxae and trochanters orange; fore femora black, with about the proximal third yellow; tibiae yellow, narrowly blackened basally, the tips more broadly so; tarsi black; middle and hind legs with the femora yellow, with about the apical third black, tibiae and tarsi about as on fore legs; posterior tibia conspicuously dilated at apex. Wings whitened, patterned with dark brown, including a band over the cord and the somewhat broader wing tip; additional small isolated dark spots at origin of R_s, vein R_3, outer end of cell 1st M_2 and tip of vein 2nd A; vague dusky washes in cell Cu and the adjoining part of cell M; stigma oval, darker than the remaining pattern; veins brown. Venation: Sc long, Sc_1 ending about opposite three-fourths the length of R_s, Sc_2 far from its tip, at near one-seventh the length of R_s; R_2 about four times R_{2+3+4}; cell 1st M_2 rectangular, subequal to the distal section of vein M_3; m-cu about one-third its length beyond fork of M.

Abdomen, including hypopygium, black, the posterior borders of segments two to six narrowly pale. Sternal pocket of fifth segment very large, broad, with unusually abundant black setae surrounding a central glandular area; sixth sternite with nearly a dozen strong setae on either side of the midline. Male hypopygium with the basistyle produced beyond the point of insertion of the dististyles as a narrow blunt-tipped lobe. Outer dististyle a narrow parallel-sided black blade, its tip bent at a right angle into a sharp spine. Inner dististyle very complex, in general bilobed, the outer lobe a strong curved spine that bears a small point on its face at near mid-length; lower lobe slender, narrowed to the obtuse blackened tip; in the axil between the major branches with a strong acute spine.

Habitat: Japan (Honshu). *Holotype:* ♂, Mount Takao, Musashi, May 13, 1950 (Inoue).

This distinct fly is named for Mr. Hiroshi Inoue, well-known Japanese Lepidopterist, to whom I am indebted for many desirable Tipulidae from various parts of Honshu. The only other regional member of the subgenus is *Teucholabis* (*Paratropesa*) *esakii* (Alexander), of northern Japan, which differs in the coloration of the body, legs and wings, and, especially, in the distinctive sternal pockets of the fifth abdominal segment and the structure of the male hypopygium, including the apical spine of the lobe of the basistyle and the much simpler structure of the inner dististyle.

NOTES AND OBSERVATIONS ON THE BIOLOGY AND REARING OF CREOPHILUS MAXILLOSUS (L.) (COLEOPTERA, STAPHYLINIDAE)[1]

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INTRODUCTION

On April 13, 1947, a single live female of *Creophilus maxillosus* (L.) collected from the carcass of a squirrel in Urbana, Illinois, was placed in a battery jar partially filled with an inch or two of black earth. On April 18 four more of these beetles (sex undetermined) were obtained from the same carcass and placed in a separate battery jar. By April 20 several white oval eggs were conspicuous against the black earth, having been dropped at random in the first battery jar; and by April 22, additional eggs had been obtained from both jars, and small but active first instar larvae were seen in the first jar. I attempted to rear these larvae through to adults for the pleasure of observing the life cycle. This was easily done, and during the subsequent 1½ months eggs were reared through to adults, the reared adults were mated, and eggs again obtained. During this time between 60 and 70 larvae were reared, some of which devoured one another at various stages before I learned to isolate them. These beetles were kept near my desk at room temperature, and various observations were made and recorded. Since I have had some requests concerning this information, much of which has not previously been recorded, these observations are presented now, although additional study remains to be done.

Considering its size, prevalence, and wide distribution, *Creophilus maxillosus* has been relatively little studied. Selous (1911) early called attention to the fact that some of the so-called carrion feeding beetles, including *C. maxillosus*, are not true carrion feeders, but that they take their food from the rich harvest of larvae which appear rapidly in any carcass. Davis (1915), using a freshly killed porcupine as bait, attracted *C. maxillosus* and several silphids to the remains. He often observed this staphylinid beetle, as well as the silphids, running about the remains with maggots in their mandibles, and estimated that these beetles "devoured thousands of the larvae". Blackwelder (1936), who studied the comparative morphology of the family Staphylinidae, provided a detailed account of the external anatomy of this adult beetle. Talbot (1928) studied the gross anatomy and histology of the adult alimentary canal. Abbott (1938), who was apparently the first to rear these insects and provide some account of their general biology and developmental behavior, found that the total duration of development from the deposition of the eggs to the emergence of the adults was approximately 37 days. More recently Fichter (1949) reemphasized the necrophilous as opposed to the necrophagous habit of a majority of the coleopterous insects found in association with carrion, and made some interesting observations on the food habits of *Creophilus maxillosus* (L.). Mank (1923) and Voris (1934), who have contributed the best detailed studies on the biology of the Staphylinidae, have not, however, dealt with *C. maxillosus*.

REARING METHODS

Isolated females, or paired males and females, obtained from the field, were placed in separate Petri dishes to which a thin layer of moist black earth had been added. These were numbered and dated. The earth provided an easy method of maintaining a suitable humidity, and from day to day a few drops of water were added to the earth with a medicine dropper when needed. (The earth would change to a lighter color as it began to dry.) Water added should keep the earth moist looking, but should not wet the Petri dish. The ordinary glass Petri dish cover sufficed to retain the moisture for a considerable period and permitted an ample oxygen supply. The black earth had the further advantage of enabling one to detect eggs easily.

During this time the adult beetles were fed daily on dipterous larvae, each beetle eating from two to six larvae per day. These were at first obtained from the field every few days from the same squirrel carcass, but later house fly larvae and pupae, reared in the university insectary, were utilized. Prolonged rearing of these beetles on any scale would undoubtedly require keeping a housefly culture.

The beetle larvae were fed in a similar fashion, by dropping fly larvae into the dishes in which they were kept. Third stage larvae could easily manage the larger maggots, but smaller maggots were utilized for the first and second instars. Living, actively wriggling larvae were used, as both adults and larvae seemed to prefer active prey. It was discovered, however, that the beetle larvae would also feed on bits of maimed larvae if they ran over them while still moist, or on pupae which had been broken open. Such pupal tissue was also hand fed to the first stage larvae within a few hours after emergence from the egg by holding it in front of the larva's mouthparts with a pair of forceps. This initial hand feeding seemed to aid in many cases in getting the isolated larvae actively started on their development.

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OBSERVATIONS ON THE LIFE CYCLE

Egg. The eggs are oval in shape, 2–3 mm. in length, milky white in color, and are dropped individually and at random on the surface of the earth. The eggs hatch in approximately 3 days at room remperature. In one instance in which the deposition and hatching of an egg were observed, the incubation period was 73 hours. The larvae apparently push and chew their way through the egg chorion in irregular fashion, as evidenced by the empty egg shells in FIG. 1.

Larvae. First stage larvae are entirely white when they hatch from the egg. The dorsal sclerites of the thorax and abdomen take on a grey color within three-quarters of an hour after hatching, while the head is a light reddish tan color. Within 1½ hours the dorsal sclerites

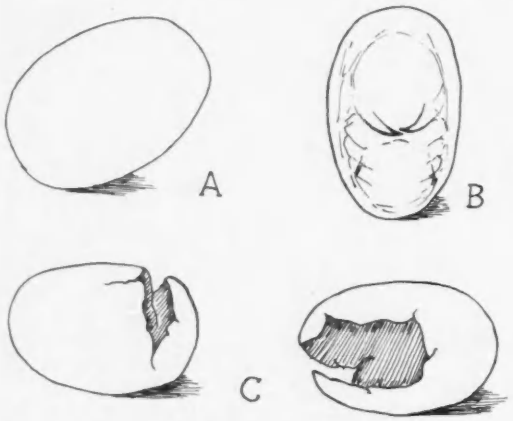

FIG. 1. Eggs of *Creophilus maxillosus.* A, shortly after oviposition; B, prior to hatching; C, egg shells from which larvae have emerged.

are dark grey and the head capsule is a dark red-brown color. The larvae are quite active when first hatched, and avidly take food within several hours after hatching, in the form of histolyzed house fly pupal tissue gently placed in front of their mouthparts. These larvae could often be reared right through the first instar by allowing them to engorge themselves 3 or 4 times on such food. Even when fed, however, the larvae must be individually isolated at once, to avoid their attacking and devouring each other on contact in their active wandering about. In one instance a Petri dish containing a dozen first stage larvae was reduced to three in number within two days. Abbott reported an instance in which he obtained only five adults from 30 larvae, as the result of cannibalism. First stage larvae molted with regularity in from 2–2½ days after hatching from the egg. These larvae use their mandibles not only for grasping their prey, but in moving particles of earth and small pebbles from place to place. In dragging off their prey the last abdominal segment is hooked into the earth or behind a stone for added support.

Second stage larvae showed almost no difference from the first instar forms apart from an increase in size. The larvae were equally as active and aggressive, feeding readily on small maggots. On one occasion I noted a second instar larva crush the head capsule of a freshly killed adult house fly with its sharp pointed mandibles, chew up the tissues and suck out the juices. The duration of the second stadium was approximately that of the first, and they molted with regularity in from 2–3 days into third instar larvae.

The third and last larval stadium differs in two respects from the two previous ones. Its duration is considerably longer, requiring from 12–15 days to pupation. Secondly there is a marked quiescent stage of from 1½ to 2 days' duration just prior to pupation. During this time the larva lies partially curled, often on its side, and for the most part is unable to move about, as frequent prodding demonstrated. In this condition the larva might twist or wiggle, but it could make no use of its legs, which seemed distended and no longer under control. If available, the larva would curl under a small stone or leaf during this quiescent stage, and lie in the nest-like hollow it forms there until pupation. With no cover available, however, larvae would become quiescent and pupate on the surface of the earth in the dish.

Pupa. The pupa emerges from the larval skin white in color and turns a light brownish color in from 1–2 hours. The newly emerged white pupa can wiggle and twist its abdomen fairly actively, but the later brownish colored pupa is quiet and does not move when disturbed. The length of the pupal stage varied from 9–11 days.

Emergence of the Adult. The head capsule and pronotum of the developing adult become darkly pigmented within the pupal case some 48 hours before the adult hatches. This darkening process spreads through the developing adult which becomes entirely dark some 24 hours before emerging. These color changes can readily be seen through the pupal cuticle, and serve as guides to the subsequent initiation of eclosion.

In one instance the adult first began to push its head out of the pupal case while lying on its side. It then succeeded in withdrawing and freeing its legs. Although a part of the pupal case still remained attached to the head, it brushed this off with its legs, wiggled itself further out of the pupal case, then fell over on its venter and crawled out of the remainder of the case. This entire process occupied approximately three minutes. The posterior wing pads were crumpled, but within 21 minutes after its hatching activities were begun,

the hind wings were fully inflated and extended over the abdomen. Scattered, small liquid droplets were visible on the extended wings, but these evaporated shortly.

On emergence the adult is completely black except for a few yellow markings and the fore wings which are white. The abbreviated forewings turn black in color within three hours. The hind wings continue to be carried extended over the abdomen for some time, but are tucked under the elytra in from 8–12 hours after emergence.

Mating behavior. Adult males and females are able and ready to copulate within 24 hours after emergence, possibly even sooner. In one instance, a reared male and reared female, both of which had emerged on May 20, were placed together in a Petri dish on May 21. These were seen end to end with their genitalia in copula within two minutes after being placed together. initial copulation lasted for one minute and 45 seconds, before being broken. The male tried to mount the female again several minutes later, but was unsuccessful.

The rapidity with which males will clasp females is emphasized by another instance. In the early summer of 1952, in Madison, Wisconsin, I obtained a male of this beetle from the field and dropped him into a dish containing a previously captured female. The male ran rapidly to the side of the dish and then began to scurry somewhat frantically around the perimeter. He had coursed over about approximately one-third the circumference of the dish when his escape efforts carried him flush over the back of the female which rested unmoving in his path. Although moving rapidly, he made a dead stop when directly over the female, and within 2 seconds had everted his genitalia and was in copula with the female. This copulation lasted

TABLE I

EMERGENCE DATES FOR LARVAL INSTARS, QUIESCENT STAGE, PUPATION AND ADULTS

SPECIMEN NUMBER	1ST LARVAL INSTAR HATCHED	2ND LARVAL INSTAR	3RD LARVAL INSTAR	QUIESCENT STAGE	PUPATION	ADULT EMERGED	TOTAL DAYS* TO ADULT
1	4/21	4/23	4/25	5/7—PM	5/9—AM	5/18—2P	27
2	4/21	4/23—9P	4/26—10A		5/11—9A	5/20—3P	29
3	4/21	4/24—AM		5/8	5/9—AM	5/18	27
10	4/23—12M	4/25—10A	4/28—6A	5/8	5/10—4P	5/20—9P	27+
12	4/23—AM	4/24—9P	4/27—4P		5/11—11A	5/21—4P	28+
13	4/23—AM	4/25—10A	4/28—6A	5/8	5/10—2P		
14	4/23—AM	4/24—9P			5/13—AM	5/22—10P	29+
16	4/23—AM	4/24—9P	4/27—1P		5/12—8A		
17	4/23	4/25—PM	4/28—1P		5/10—2P	5/20—8P	27
18	4/23	4/25—10A	4/28—GA		5/11—8A	5/20—12M	27
19	4/23	4/25	4/28—6A		5/12—10A	5/22—12M	29
20	4/24—AM	4/26—10A			5/13—AM	5/22—1P	28

*The egg incubation period would bring the total developmental period to between 30–33 days.

In another instance reared males and females, both of which had emerged on May 18, were placed together in a Petri dish on May 21. Again the initial copulation took place within several minutes after introducing the male. The male approached the female from the rear, and quite suddenly attempted to mount the back of the female. In this attempt there was a struggle with both male and female twisting and turning over. On the first two tries the female managed to escape, but on the third attempt the male was successful in mounting and grasping the back of the female, and within 2–3 seconds had his genitalia everted and clasped to those of the female. A few seconds after this the male released his legs from the back of the female and turned off to the right so that they were end to end, with their genitalia still clasped. At this the female attempted to run off, but the male, after being dragged a short distance, held on to a leaf and retarded the female. This more than ten minutes so that the brief copulations noted above are not normal. Abbot (1938) noted matings that lasted at least an hour.

Oviposition. No previous records are available regarding either the number of eggs laid, or the duration of the oviposition period. In one instance a female brought in from the field and isolated in a Petri dish on April 24 produced a total of 68 eggs over a period of 32 days, the number of eggs ranging from as many as 14 eggs over a single 24 hour period to as little as a single egg over a period of six days (see Table II). It is possible that oviposition in the field may continue at the high level of the first few days recorded here so long as an abundant food supply is available. As was previously mentioned, eggs are dropped on the earth at random in the Petri dish and battery jar containers. It remains to be determined whether or not other means of egg disposal occur in the field.

In the case of the reared adults mentioned

above (emerged May 20 and mating observed on May 21) the first egg deposited was observed the evening of May 24. Thirteen additional eggs were deposited by May 26; 5 more eggs by May 27; 2 eggs on May 28; 4 eggs on May 29; 1 egg on May 31; and 2 eggs on June 1—a total of 28 eggs over a nine-day period. Further observations on this pair were, of necessity, discontinued. Thus oviposition may occur at least as soon as four days after the emergence of the adult female.

mediately after molting, all prior to any food intake. The weight of the first larval instar ranged from 2.5–3.4 mgms; that of the second instars from 7.4–15.3 mgms; that of the third instars from 28.7–54.3 mgms; and that of the pupae from 105.1–178.5 mgms. (Table III). On the basis of the average weights obtained there was a 4.0 x increase of weight of the second larval instar over the first, a 3.2 x increase of weight of the third larval instar over that of the second instar; and a 3.6 x increase of weight of

TABLE II

OVIPOSITION OF A SINGLE OBSERVED FEMALE

															TOTAL
DATE	4/25	4/26	4/27	4/28	4/30	5/4	5/10	5/13	5/15	5/21	5/22	5/23	5/25	5/27	32 DAYS
No. Eggs	14	10	6	2	9	2	4	4	2	1	2	8	3	1	68

TABLE III

WEIGHT, IN MILLIGRAMS, OF LARVAL INSTARS AND PUPA ON EMERGENCE

SPECIMEN NUMBER.	1ST LARVAL INSTAR	2ND LARVAL INSTAR	3RD LARVAL INSTAR	PUPA	SEX
1			33.3	116.3	♀
2			41.3	150.1	♀
3			30.4	128.7	♂
9			39.3		
10		11.9	47.4	152.8	♂
11		15.3			
12		17.2	46.8	178.5	♂
13		17.0		174.7	
14		10.9	41.6	125.3	♀
15		10.8			
16		14.9	41.0	126.6	
17		12.5	35.1	154.7	♂
18		13.7	45.9	132.3	♀
19		9.1	34.3	138.2	♂
20		7.4		129.8	♂
21	3.2				
22	3.1				
23	3.4	11.4	31.6		
24	2.5	11.4	15.9		
25	2.5	7.5			
26			44.1		
28		8.7	38.5		
31	2.9	13.2	47.5	132.2	♀
32	2.8		43.2	129.6	♀
33	3.2	14.0	54.3	158.3	♂
34	3.1				
35	3.4		28.7	105.1	♀
Average Wt.....	3.01	12.17	38.94	139.56	

Weight Increase of Instars. Some information concerning the increase in weight which takes place through the larval and the pupal instar was obtained by weighing 27 individuals (see Table III). Weighings were uniformly carried out on a chemical type analytical balance to the nearest tenth milligram, either immediately after the first larval instar hatched from the egg, or im-

the pupa over the third larval instars or a 46.1 x total increase of weight from hatching to pupation.

Longevity. Adult beetles brought in from the field remained alive in captivity from 30–35 days. Adult females tended to outlive the males, but this was sometimes due to the fact that the adult males were eventually attacked and eaten by the females.

DISCUSSION

In view of the ease with which these insects may be reared through their complete life cycle in the laboratory, and the readiness with which adults may be obtained in the field, it is surprising that more attention has not been given to their general biology. *C. maxillosus* would seem to possess much potentiality as a laboratory insect for physiological and further behavior studies.

Other investigators have called attention to the ease with which several other species of staphylinids may be reared in the laboratory. Mank (1923) raised twenty adult staphylinid beetles from larvae. These included *Philonthus brunneus* (Grav.), *P. longicornis* Steph., *P. cyannipennis* (Fab.), *Tachinus flavipennis* Dej and *Belonochus formosus* (Grav.). Both larvae and adults were kept in small tin salve boxes, half filled with moist sand, to which was added from time to time, disintegrating vegetable material containing dipterous larvae and mites on which the beetle larvae fed. She remarked on how easily, over a six weeks' period, these larvae were reared to adults in these small containers.

Wadsworth (1915) mentioned that the adult *Aleochara bilineata*, parasitic on the puparia of cabbage flies, lived quite well in captivity. He kept individuals alive for three months, and experienced no difficulty in obtaining fertile females, ova, and larvae for the observation of the complete developmental cycle in the laboratory. He obtained his adults by collecting puparia of the cabbage fly, containing first stage larvae, during the winter months and rearing these to adults at room temperature. This he was able to do in one month's time.

Schaup (1878), who was early active in rearing many coleopterous larvae, succeeded in rearing *Staphilinus maculosus* and a few other staphylinid larvae collected in the field. Voris (1934) mentions obtaining twelve eggs over a 22-day period from a pair of *Staphilinus maculosus* taken in the field and placed together in a small jar partially filled with earth. I kept an adult *Staphylinus sp.*, which I fed maggots from day to day, in the laboratory in a small dish for three weeks. After the first week, as soon as the glass cover of the culture dish was moved, this beetle would become alert, and would raise its head upward and grab the maggot from my forceps with its mandibles as soon as it was within striking distance of its mouthparts. This form is larger and even more active than *Creophilus maxillosus*.

Voris (1934) who reared through to adulthood large numbers of larval *Philonthus cruentatus* (Gmel.), *P. tetragenocephalus* Notman and *Quedius capucinus* (Grav.) indicated that the most important factor in maintaining satisfactory cultures was the proper amount of moisture. In rearing *C. maxillosus*, this requirement seems to be most readily met by keeping a bed of moist but not wet earth in the culture dish. Rau (1922) observed adult *C. maxillosus* drinking up an accumulation of juices from a dead mouse placed in the container in which the beetles were kept. This drinking behavior seems otherwise to have escaped notice. I have often fed drops of water to adult beetles which they sucked up avidly when gently placed before their mouthparts at the end of a pair of forceps, particularly if the culture dish was partially dried, or the adults had not received food for a period of a day.

Creophilus maxillosus adults are easily obtained from carcasses in the field, or carcasses may be placed in the field as bait. I have also obtained them in large numbers underneath and around animal refuse cans near the University of Wisconsin animal house in Madison, apparently living on the fly larvae often to be found there. Talbot (1928) reports finding them in and around an open shed of a meat packing house in Columbus, Ohio, where fly larvae were abundant in the masses of animal hair there. Various authors have reported finding them in early spring, summer, or early fall.

SUMMARY

1. Adult *Creophilus maxillosus* taken in the field can be kept alive in the laboratory in Petri dishes, or other suitable containers partially filled with moist earth. Adults fed on a diet of dipterous larvae will pair, and eggs can be obtained. These may be reared through the complete life cycle.

2. When kept at room temperature, the complete life cycle from deposition of eggs to the emergence of adults requires from 30–33 days, as follows:—egg incubation—3 days; first larval stadium—2–2½ days; second stadium—2–3 days; third stadium—12–15 days (including a prepupal quiescent stage of 1½–2 days); pupation—9–11 days.

3. Observations on mating and other behavior, as well as a discussion concerning other staphylinids which may be reared in the laboratory are included.

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[2]NOTE: According to Dr. Richard E. Blackwelder (correspondence, 1955) there is only a single species, *Creophilus maxillosus* (L.) in the entire Holarctic region. This species is found as far south as Guatemala, Jamaica, and India. Although there is considerable variation in museum dried specimens, forms from Europe, Alaska, and Jamaica cannot be told apart with any certainty. Gravenhorst, in Germany, obtained specimens from this country and apparently thinking that they must necessarily be different from the European species, named the species from the United States *C. villosus* (Gravenhorst). State collected specimens in the U. S. National Museum, ranging from East to West show variation, but no definite species or variety distinctions. A modern critical taxonomic study has not yet been made to determine whether more than one species is actually present in this country. (See Blackwelder, 1943, p. 449).

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SEASONAL DISTRIBUTION AND LIFE CYCLES OF EPHEMEROPTERA[1]

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The seasonal distribution and life cycles are recorded for relatively few species of mayflies occurring in lakes. Such knowledge is limited primarily to species of the genera *Hexagenia* and *Ephemera* (Neave 1932; Spieth 1936; Berner, 1950). The present paper presents data on seasonal distribution and life cycles of 22 species obtained during a four-season ecological study of mayflies of Douglas Lake, Cheboygan County, Michigan.

METHODS

The main portion of the field work covered a period of four consecutive summers. To supplement the summer material, collections were made in the spring at two-week intervals following the disappearance of the ice cover and also during the fall. A total of 240 collections, including approximately 25,000 specimens, were taken. Both nymphs and adults were preserved in 80 percent ethyl or isopropyl alcohol; however, representative adults were preserved dry on pins or in papers.

Collecting equipment consisted of circular pan screens (20 and 30 mesh) for sifting bottom materials and washings from stones. In deeper water a long-handled, aquatic dip-net, a triangular-mouth tow dredge, or an Ekman dredge was used to bring up aquatic plants and bottom materials which were then screened. To obtain nymphs less than 3 mm. in length, unsifted bottom materials were brought to the laboratory and examined under magnification.

In making collections from any one habitat, population samples were taken either along a line transect from the shore line into the deeper water or by random selection at various depths. Because of the scarcity of nymphs of certain species, and because of the reduction in numbers of a better represented species toward the end of an emergence period, a thorough search was made in selected favorable habitats to determine the presence or absence of nymphs. Observations on swarming of adults were made whenever possible. Vegetation along the shore was examined for adults whenever collections of nymphs were made.

The terms *abundant*, *common*, *scarce*, and *rare* as used in this paper designate relative numbers of individuals and refer to one species as compared with all others in Douglas Lake but not as compared to those of other lakes. Since general descriptions of Douglas Lake are already available elsewhere (Scott 1921; Welch 1928; Eggleton 1931; Moffett 1943), it seems unnecessary to review this subject again; however, a map of Douglas Lake (FIG. 1) is included to show the specific locations referred to in this paper.

DISCUSSION

A graphic summary of the emergence periods of Douglas Lake mayflies is presented in Table I and in the following section the life cycle and seasonal distribution is discussed for each species using the order of taxonomic sequence given by Needham, Traver, Hsu (1935).

Ephemera simulans Walker

The imagoes of *Ephemera simulans* are fairly common around the shore of Douglas Lake during two months of the year. The emergence period extends from about June 10 to August 1, the maximum number of adults appearing in early to middle July.

Interesting comparisons may be made on the relative length of the emergence period of this species in various localities. Eaton (1883) and

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Burks (1953) have reported the enormous swarms which appear yearly from Lake Michigan at Chicago, Illinois, about the third week in July. Clemens (1915) has given June 5 to July 27 as collection dates for *E. simulans* in the Georgian Bay region. For Lake Nipissing, Ontario, Ide (1930) has stated the emergence dates June 30 to July 24. The writer has observed numerous imagoes in the vicinity of the Straits of Mackinac during June and July while in Lake Erie at Put-in-Bay, Ohio, adults were collected between June 11 and July 23 with the peak of emergence occurring about July 1. In contrast with the foregoing, Spieth (1936) has shown that in northern Indiana lakes and at Spencer, Indiana (White River), the main emergence of huge numbers of individuals of *E. simulans* is relatively short and occurs during the last of May and the first few days in June, although stragglers precede and follow this period by several days. For Illinois, Burks (1953) gives the earliest collection date of May 16 for *E. simulans*. In southern Michigan the writer has collected *E. simulans* as early as May 17 although the principal emergence usually occurs at the end of May and is of short duration. For example, during the last of May and first part of June, prodigious numbers of imagoes emerge from the Huron River near Ann Arbor, from Bass Lake in Livingston County, and from other lakes in southern Michigan.

Thus, it is observed that real differences occur in the over-all length of the emergence period of *E. simulans* over its wide geographical range. Ide (1935) has indicated already that the form of *E. simulans* inhabiting streams will eventually prove to be specifically different from the form inhabiting lakes. Although, on preliminary evidence, temperature appears to be an important factor correlated with the abundance of adults and the seasonal emergence pattern of *E. simulans*, further studies should be made to discover the reason for this phenomenon. A short emergence period in this species seems to be correlated

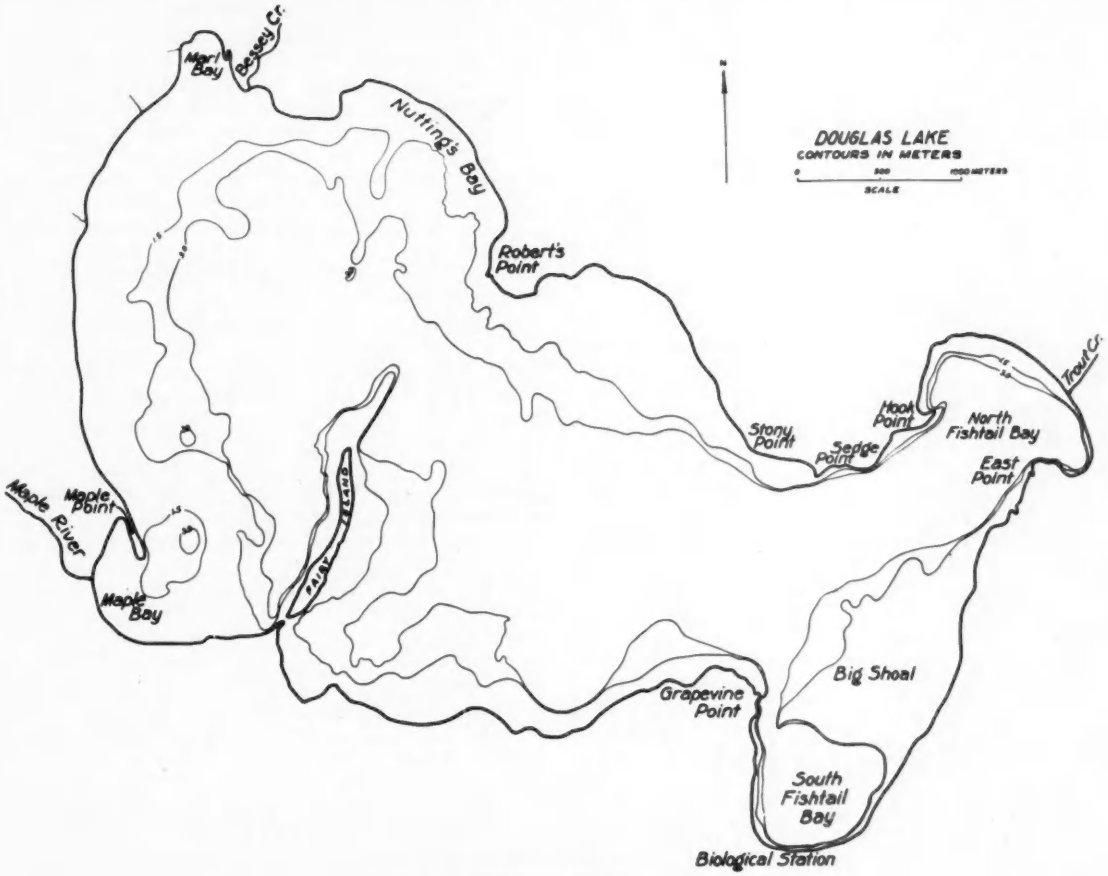

FIG. 1. Map of Douglas Lake, Michigan.

with a more southerly distribution and, consequently, a higher average water temperature over a longer seasonal period. For example, *E. simulans* emerges over a long period from the Great Lakes and from other lakes of more northerly latitudes where water temperatures are relatively colder during a shorter season of the year. On the other hand in the small, warmer bodies of water with higher average summer temperatures over a longer season, such as occurs in the lakes and streams of more southerly latitudes, *E. simulans* emerges over a relatively short period. As a result of this short emergence period, greater numbers and concentrations of adults are observed at the time of the annual seasonal emergence.

The burrowing nymphs of *E. simulans* are difficult to find and seemingly occur in comparatively small numbers in Douglas Lake. Clemens (1915) found this to be the case at Go-Home-Bay, Ontario, where, although adults were numerous, he was unable to find nymphs. Nymphs are found in Douglas Lake only as widely scattered individuals in loose, fine sand of that part of the littoral region included within the 1 and 3 meter contours. It might be emphasized that in situations where nymphs are seemingly scarce or rare, yet adults are common, these nymphs are widely distributed over a large area of the littoral zone while the emerging adults are always concentrated in a relatively narrow strip along the shore.

In Douglas Lake the life cycle of *E. simulans* is completed in one year. Mature and almost mature nymphs are present during the spring and summer until around August 1 at which time very young nymphs, a few millimeters in length, are found. Spieth (1936) also concluded that the life cycle was completed in one year in Indiana. In Bass Lake the writer found that *E. simulans* nymphs reach nearly their full growth by November. Growth essentially ceases until the following spring when final maturity of these nymphs occurs rapidly just prior to emergence.

Hexagenia limbata (Serville)

Hexagenia limbata is abundant at Douglas Lake. During the emergence period dense drifts and windrows of the bodies of imagoes and nymphal exuviae may be found floating in the water and piled along the shore. It was noted that these drifts and windrows consisted almost entirely of bodies of female imagoes with only an occasional male being found. This result arises from the fact that, following copulation, the female flies out over the water to oviposit, does not usually return to land but dies on the water. The mating flight, however, occurs over land and after copulation, the male generally alights on nearby vegetation or rejoins the swarm for further matings, ultimately dying on land rather than on water. Bodies of males are found rather commonly scattered among vegetation along the shore, whereas, in that situation, the body of a female lacking egg packets is exceedingly rare. Moreover, a living female imago without egg packets was rarely seen resting on vegetation. When specimens are collected from vegetation during the day, there

TABLE I

EMERGENCE PERIODS OF DOUGLAS LAKE MAYFLIES

SPECIES	MAY	JUNE	JULY	AUGUST	SEPTEMBER	OCTOBER
Ephemera simulans		———	-XXXX*—			
Hexagenia limbata		—X	XXX——			
Hexagenia affiliata			—X—			
Stenonema femoratum		—XXX—	—XX——	—X———		
Stenonema interpunctatum		———	—XXX——	—XX———	X——	
Heptagenia lucidipennis		———	-X——			
Siphloplecton basale	—X—					
Siphlonurus rapidus	—X—					
Leptophlebia nebulosa	—X—					
Choroterpes basalis			———	—XXX——	——	
Baetisca obesa		?–X–?				
Ephemerella bicolor		——XX—				
Ephemerella lutulenta	—X——					
Ephemerella temporalis		——XX——				
Tricorythodes allectus			?—X—	—?		
Brachycercus lacustris			———	—X———	——	
Caenis simulans		—XXXX	X———	——		
Callibaetis ferrugineus		———	———	———		
Baetis phoebus		———	—XXX——	———	———	———
Centroptilum fragile		——	—XX——	———		
Pseudocloeon dubium		——	-XX——	———		
Cloeon rubropictum		—XX	XXXXXX	XX———	———	——

*X indicates time of greatest abundance.

is a conspicuous preponderance of males over females. Yet, at the height of the emergence period the windrows of a morning, following a large swarming of an evening before, will consist primarily of prodigious numbers of females. This apparent difference in number may be due either to more secretive habits of females during the day or to longer life of the male. The latter alternative would result in an accumulation of males present.

During the four seasons it was observed that the largest emergence occurred in the summer of 1938 while the emergences of 1936, 1937, and 1939 were much smaller but more or less equal in relative numbers of individuals. Also, this large emergence was correlated with Ekman dredge samples taken during the summer of 1937 which contained more nymphs per dredge than did similar samples during either of the subsequent years. A cyclical trend in population numbers was also observed for *Hexagenia* in Lake Erie (Lyman 1944a).

The emergence of *H. limbata* occurs from about June 15 to July 20 with a maximum between June 20 and July 5. At the beginning of the emergence period the surface-water temperature ranges between 18° and 20° C. and by July 1 the temperature varies around 21°–22° C. The subimago usually emerges from the nymph during the early morning and after a quiet night, the lake surface will be found speckled with cast skins of nymphs floating on the calm water. The subimago period covers 36–48 hours depending to a large degree upon the air temperature and weather conditions (Lyman 1944). If the weather is warm and fair, the period is shortened, whereas it is lengthened by cold and rainy conditions.

The swarming or mating flight of *H. limbata* takes place over land in the evening. The nature of the swarm depends upon wind and other weather conditions. During cloudy, windy, or rainy weather, swarming is more or less sporadic and confined to small groups in well-protected situations. The most favorable time appears to be during calm, fair, and warm weather or when only a slight breeze is blowing.

Large swarms were observed mainly during the last of June over Grapevine Point. During the sunny hours of the day most of the imagoes rest quietly on the underside of leaves; those on the upper surface are in densely shaded areas. As the sun approaches the horizon they begin to move more and more to the upperside of the leaves. Early on a calm evening the foliage is literally covered by thousands of imagoes. As the light fades a restless stirring developes and here and there an individual leaves its resting place for another, usually a little higher. If a breeze begins to move the leaves, a few males take wing and soon a large number of them are flying low over small open areas of low vegetation. Should this breeze cease, they gradually settle again on the vegetation and remain there until the main swarming begins at about 9:00 p.m. (E.S.T.). If the breeze persists, the swarming continues although females do not approach the swarm until much later. On a completely calm evening, swarming does not take place earlier than 9:00 p.m. At 8:55 p.m. a few males begin to swarm over the low trees and shrubs. Within two minutes hundreds are in the air and by 9:00 p.m. thousands of males are swarming. Thus, the number of individuals taking part in a swarm increases rapidly in a remarkably short length of time. At first the swarm flies just above the lowest small trees and shrubs in the more or less open areas in the surrounding woods and numerous specimens come within easy reach of the insect net. As the light fades, the swarm rises gradually higher and higher. By 9:20 p.m. all members of the swarm are well out of reach of a net and concentrated slightly above the tops of the highest trees fringing the lake shore. Females enter the swarm from time to time from the surrounding vegetation. They do not fly up and float down as do the males but fly in a more or less zigzag oblique course upward through the swarm until grasped by a male. The swarming continues until well after 9:30 p.m. when darkness makes impossible further observations. Only females in flight and in oviposition were observed over the deeper waters between 9:30 and 10:00 p.m. but no males were seen at this time flying over the lake. The main swarming of males takes place along the shore of the lake over the tops of the trees, not over the open areas along the shore or out over the lake. At Put-in-Bay, Ohio, in Lake Erie swarming activities of *Hexagenia* begin about one hour earlier than at Douglas Lake (Lyman 1944a) which seems to indicate that there may be a correlation between the initiation of the mating flight and light intensity. The factors involved in initiating the mating flight of mayflies need more investigation.

The burrowing nymphs of *H. limbata* may be found in Douglas Lake at water depths of 1–15 meters. Those specimens taken in shallower depths (1–6 meters) were usually very young, recently hatched nymphs or those of comparatively small size (up to 10 mm.). Nymphs of larger size were very rarely encountered on sandy bottoms in shallow water. The greatest number of large specimens (20–25 mm.) were taken in soft mud at water depths of 11–13 meters on the west side of South Fishtail Bay and opposite Grapevine Point proper. They occur at 8–10 meters in North Fishtail Bay near Hook Point. In this area the transition from sandy to muddy bottom begins at a shallower depth than in South Fishtail Bay. The reasons for the restriction of *Hexagenia* nymphs to muddy

bottoms and to water depths not greater than 15 meters were given in a previous paper (Lyman 1943). The largest number of nymphs collected in a single haul with a 15 x 15 cm. Ekman dredge in Douglas Lake was 6 and often many samples taken at a given depth contained no nymphs. In comparison, Neave (1932) recorded taking 401 nymphs of *Hexagenia* in 10 hauls of a 23 x 23 cm. Ekman dredge from Lake Winnipeg.

In Douglas Lake the length of the life cycle of *H. limbata* is two years (FIG. 2). This substantiates the same conclusion reached by Neave (1932) for this species in Lake Winnipeg. It

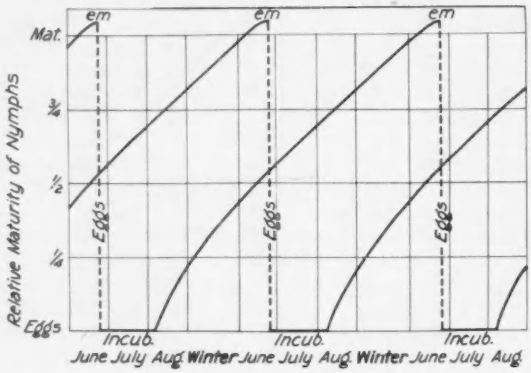

FIG. 2. Diagrammatic representation of seasonal life cycle of *Hexagenia limbata* in Douglas Lake. Mat.—mature nymphs; em—emergence; incub.—incubation period of eggs.

should be stressed, however, that not all species of the genus *Hexagenia* have a life cycle of two years (Lyman 1943a). Eggs are deposited in Douglas Lake during late June and early July and very young nymphs which hatch from these eggs are found during early August. Thus, the approximate length of the incubation period under natural conditions agrees well with Hunt (1951) who found that *H. limbata* eggs hatched in 20–26 days under laboratory conditions at a temperature range of 62°–73° F. At the beginning of the following summer these nymphs have become half grown, and by late August they are almost fully grown and emerge the next summer. The basis for this conclusion is that following the emergence of early summer, numerous nymphs, about three-fourths grown, but no fully mature nymphs, may be found during July and August (FIG. 2), while in August, the very small recently hatched nymphs are found. Thus, two distinct age groups are present at this time of year and continue until the following summer when emergence of the older one occurs.

Hexagenia affiliata McDunnough

The earliest date of collection of *Hexagenia affiliata* was July 10, the latest July 31. This species is rare, since the total number of specimens collected was 25. All adults were taken in the vicinity of South Fishtail Bay resting on vegetation and none were taken from swarms. No nymphs known to be of this species were found.

Stenonema femoratum (Say)

Stenonema femoratum is one of the most abundant species around Douglas Lake throughout most of the summer. Imagoes are particularly numerous from about June 5 to July 15 although specimens may be found from the last of May to the end of August. During the day they usually rest on vegetation close to the water's edge. Swarming of males and mating take place between 7:30 and 9:00 p.m. along the shore of the lake over both land and water. No swarms were observed during the day. Swarming in this species stops at approximately the same time that the swarming of *Stenonema interpunctatum*. begins. From reared specimens the length of the subimago period was determined as approximately 24 hours but this period is lengthened by a spell of cool weather (Lyman 1944).

The life cycle of *S. femoratum* in Douglas Lake is completed in one year. The long emergence period is best represented by a trimodal seasonal curve the peaks of which represent three periods of relative abundance of the adults as shown in FIGURE 3. The nymphs are present in large numbers at all seasons of the year in the shallow

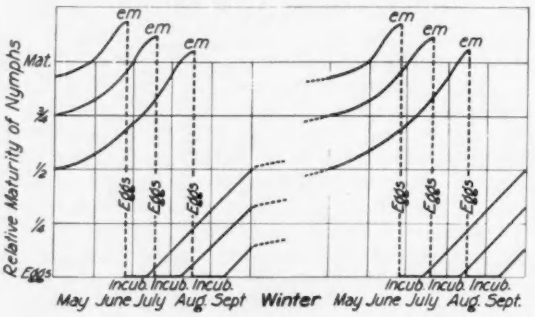

FIG. 3. Diagrammatic representation of the seasonal life cycle of *Stenonema femoratum*. Height of curve above maturity line indicates relative size of the emergence. Mat—mature nymphs; em—emergence; incub—incubation period of eggs.

littoral region wherever rocks or other similar objects are present. Collections of nymphs in May consist mainly of mature or almost mature specimens; however, many smaller nymphs are also present and the entire size range of all collected was from about one-half grown to fully mature. The degree of maturity was determined from the length and development of

the wing pads, since nymphs ready to emerge have large, much darkened wing pads, while in earlier instars, they are smaller and light colored. In May there appear to be three distinct age and size groups, all of which have come from eggs deposited at different times during the previous summer. Of these three groups of nymphs, the first emerges during June and early July, is the largest in number and size of individuals, and produces the largest emergence of the summer. The second group which emerges during July is the next in size and in number of individuals, while the third group which comes in August is the smallest in number and size of individuals. These facts are supported by collections taken throughout the summer. Such collections show two distinct groups of nymphs maturing, one in mid-July and the other in mid-August. No mature nymphs, or adults, were ever taken after late August. The three groups are also correlated with swarming activity of adults and the relative abundance of individuals found at different times during the summer. Although from collections of imagoes alone, the conclusion might be reached that there is only a single, long, unimodal emergence period rather than three more or less distinct ones, each relatively smaller than the previous one. Also, collections taken in September and October show three distinct size groups coming from eggs deposited by each of the three groups present in the spring and which matured separately at three different times during the summer. According to Needham, Traver, Hsu (1935) the incubation period of the eggs of *S. tripunctatum* (= *S. femoratum*) is 11–23 days under laboratory conditions, which time coincides with field observations at Douglas Lake. Eggs laid in June hatch during July, since collections taken in mid-July consist of numerous newly hatched, three-fourths mature, and fully mature nymphs. Collections made in mid-August consist of numerous recently hatched, one-fourth mature, and a few mature nymphs.

Stenonema interpunctatum (Say)

Stenonema interpunctatum is common to abundant during most of the summer. Imagoes were collected either on vegetation or in swarm from about June 15 to September 15. The maximum of abundance is reached about July 15. A smaller emergence occurs during early August and a still smaller one consisting of comparatively few individuals takes place in late August and early September. Adults of *S. interpunctatum* seem to be more numerous on vegetation farther back from the shore line while *S. femoratum* is usually found on vegetation near the shore line.

Swarming of males in this species occurs at dusk in the evening over a comparatively short period of time. In July, swarming of the males does not begin until almost 9:00 p.m. and lasts until dark (9:30 p.m.). Females were seen to enter the swarm about 9:15 p.m. but not before. This species seems to swarm with more regularity each evening from day to day, whereas, *S. femoratum* swarms one evening and then may not be seen again for several days. Both *S. interpunctatum* and *S. femoratum* have the same general type of swarming flight, which consists of hovering in one place for a time then darting elsewhere. Neither of these two species flies up and glides down in the type of flight characteristic of *Ephemera* and *Hexagenia*. *S. femoratum* appears to have a slower flight than *S. interpunctatum* and was often seen swarming over land close to the shore line while *S. interpunctatum* was always observed over water near the shore line but not over land.

The nymphs of *S. interpunctatum* are present in relatively large numbers at all seasons of the year in the littoral region in such situations as Grapevine Point and Fairy Island where rocks are numerous. They are most abundant in deeper water (1–2 meters) and are much less numerous close to the shore line. They are less widely distributed than *S. femoratum* and are very rare at Hook Point, Marl Bay, and Stony Point where the latter species is common. These nymphs do not occur under isolated stones, old boards, or logs unless these objects are close to a rocky situation.

The life cycle is undoubtedly completed in one year in Douglas Lake and the pattern follows closely that of *S. femoratum*. Wodsedalek (1912) inferred that the life cycle required two years, a supposition which appears now to be incorrect. Collections of numerous individuals in late May show three age groups of nymphs which may be arbitrarily classified as approximately three-fourths, one-half, and one-fourth mature. Likewise, October collections contain three age groups but the largest nymphs are not more than about one-half mature and the smallest nymphs are those which recently hatched from eggs laid in late summer. There appears to be very little growth of nymphs during the winter months for nymphs collected early in May are only slightly larger than those collected in October. It thus seems that there is a marked increase in growth rate in the late spring, for the largest nymphs taken in early May are a little more than half grown yet they emerge during the last half of June and early July. Eggs of these individuals begin to hatch late in July and the nymphs become about one-half grown before winter when growth all but stops.

Heptagenia lucidipennis (Clemens)

Representatives of *Heptagenia lucidipennis* are relatively uncommon and imagoes were collected from vegetation along shore in only two localities, Fairy Island and Stony Point. No

specimens were seen or taken in swarm. The emergence period is comparatively short and distinct and occurs from about June 25 to July 20 with a maximum of abundance around July 10.

The nymphs were found in numbers only on the northwest shore of Fairy Island, on Stony Point, and on Robert's Point where the rocks, lying close together, form an almost solid pavement over the bottom. A few specimens were collected at Grapevine Point and two at Hook Point.

The life cycle is completed in one year with a unimodal emergence period. On May 29 a series of nymphs was collected under stones from Fairy Island and Stony Point which averaged 1.0–1.5 mm. in length, the largest specimen being 2.5 mm. long and the smallest 1.0 mm. Twelve days later, on June 10, another series of nymphs collected from these localities averaged 5–6 mm. in length. The average size of mature nymphs is 7–8 mm. The surface-water temperature on May 29 was about 15.5° C. while on June 10 it was 20° C. Also, during this twelve-day period there was a marked increase in the growth of filamentous algae on the stones. This may be correlated with the rapid growth rate of the nymphs during this short period. An examination of the digestive tract of the nymphs collected on June 10 disclosed fragments of these filamentous algae. Although practically all nymphs collected on June 10 were of large size (5–6 mm.), a few small nymphs (2–3 mm.) were also taken. The first mature nymphs were collected about June 25 when the first imagoes were captured. The maximum abundance of both mature nymphs and adults occurs early in July. After July 20 no nymphs or imagoes were found. No nymphs of *H. lucidipennis* could be located during late summer or early fall. It thus appears that the incubation period in this species is a long one. Probably the eggs either hatch in the very late fall and the nymphs overwinter with little or no growth, or the eggs overwinter and hatch in the early spring just after the disappearance of the ice cover. Indications seem to favor the latter premise since this would account for the appearance of the scattered very small nymphs which occurred along with the large nymphs on June 10.

Siphloplecton basale (Walker)

The adults of *Siphloplecton basale* are rather common in May. This species is the first to emerge from Douglas Lake in the spring and the emergence period extends over about three weeks. Subimagoes were taken on May 12 as they emerged from the nymphal skins during the late morning while the water temperature was 15° C. and the ice cover had been off the lake for only two weeks. A male subimago taken on May 13 at 11:00 a.m. as it left the nymphal skin, emerged as an imago on May 15 at 3:00 p.m. Males were observed swarming during a cloudy afternoon when the air temperature was 14° C. There was very little wind and most of the specimens flew at a height of 4–5 meters. They have a hovering and darting type of flight with a comparatively slow wing-beat. While hovering, the body is held with the anterior portion uppermost at an angle of about 45° with the horizontal. The tails and forelegs are spread apart during hovering and are brought together as the mayfly darts from one position to another. While hovering, it may move slowly up, down, or sideways without darting. Swarms were seen only over the water just beyond the shore line in the vicinity of Grapevine Point, North Fishtail Bay, and South Fishtail Bay. Swarming was also seen in the evening about 8:00 p.m.

Nymphs were collected only during May. They were common almost everywhere around the shore of the lake: in more protected coves, along open sandy beaches, in beach pools resulting from high water. Specimens were most abundant in stands of *Scirpus americanus* which appeared to afford them with temporary shelter during the shoreward migration. Individuals were often seen, usually near the water surface, swimming shoreward through the open water. During windy periods they were more or less carried along by the waves. Thus, in one way or the other the nymphs reached the shore and either clambered out of the water or were washed-up onto the sand where they emerged. From all indications this procedure seemed to be a normal one before emergence took place since no specimens were observed emerging from the open-water surface of the lake. During late morning, subimagoes were seen in North Fishtail Bay and other parts of the lake flying up from the sandy inner beaches where they had emerged from the nymphal skins. Nymphs and cast exuviae were common on the sands of the inner beach. No nymphal skins were found floating on the water surface out in the lake. Immature nymphs of *S. basale* were not collected from the shallow littoral zone or in the emergent plant beds. It is therefore concluded that they inhabited the submerged plant beds of the deeper water. However, efforts made to collect them in such places were unsuccessful. Since these nymphs are very strong, agile swimmers, they might easily have evaded the methods used for collecting them. It appears that the nymphs, when ready to emerge, leave the submerged plant zone, and either swim to the shore or allow themselves to be washed there by the waves.

Siphlonurus rapidus McDunnough

Only the nymphs of *Siphlonurus rapidus* were collected in Douglas Lake. During the last of

May in 1938, they were found in almost every pool located close to the lake shore but were rarely taken in the lake itself. At the time collections were made most of these pools were not directly connected with the lake but were usually separated from it by a narrow, relatively low strip of land. From all indications these pools had been connected with the lake earlier in the spring when the water level was higher and the nymphs had migrated into the pools during this period of higher water and were stranded there as the water level receded. They did not occur in those pools which had had no direct connection with the lake and which had been formed only by water seepage. In May of 1939 very few specimens were found in those pools in which they had been numerous the year before and many of the pools contained none at all. The spring of 1939 was much drier than the same period of 1938.

S. rapidus nymphs occur in abundance in most of the small streams of the countryside surrounding the lake. Emergence occurs at the end of May and early June. During a period of high water when the streams become swollen and overflow their banks, the nymphs migrate from the main channel of the stream into adjacent overflow areas. Here they remain to complete their nymphal development and usually emerge successfully even though the water level of the stream may drop rapidly and leave them stranded in shallow pools or ditches. During the high-water spring of 1938 many of the nymphs were probably swept downstream into the lake and as a result were found in the pools around the lake. Presumably this did not happen in the drier spring of 1939 and therefore very few nymphs were found around the lake. Yet, they were just as abundant as previously in the various streams. All the nymphs of *S. rapidus* collected were mature or almost mature a fact which leads to the conclusion that the more immature stages are probably confined to the streams and do not occur in Douglas Lake proper.

Leptophlebia nebulosa (Walker)

The imagoes of *Leptophlebia nebulosa* are common although the period of emergence is relatively short and occurs during the last of May and the first of June. The length of the subimago period is about 24 hours.

Swarming of the males was observed in both morning and afternoon but not in the evening. It consisted of flying up and floating down more or less over one spot and usually over the shrubs or low trees fringing the shore. Several females were seen ovipositing between 9:00 and 11:00 a.m. in the vicinity of Hook Point. They flew back and forth along the shore about 3 meters above the water. From time to time an individual of the group swooped down, alighted for an instant on the water surface with wings held vertically and body resting on the water, deposited a group of eggs, and then resumed flight. This performance was repeated several times within a few minutes by the same individual until all the eggs were deposited. In some cases the abdomen was merely dipped in the water as the female skimmed along over it without alighting.

The nymphs are most common in the shallow littoral regions of the more quiet portions of the lake such as Hook Point, Marl Bay, and Maple Bay, although they do occur in typical rocky habitats in smaller numbers. The nymphs seem to be negatively phototactic as they are usually found under old wood, stones, or debris along the shore. In the spring the nymphs migrate shoreward and are usually found at the very water's edge. They do not normally occur along the open sandy shores where wave action is strong and where there is small chance for accumulation of debris. They are often found in small, shallow pools close to the shore line which are formed by high water but later become isolated from the lake proper by the drop in water level. These nymphs do not emerge from the open-water surface but clamber onto the shore and emerge 1–2 cm. above the water line. In captivity they readily eat all sorts of organic debris such as collects along shore or in the bottom of pools and they often consume the dead bodies of other nymphs or their exuviae.

Eggs laid in spring, hatch during the last of July and forepart of August. Numerous very small nymphs (1 mm.) were collected during this part of the summer. By the middle of October the nymphs attain a length of 3–4 mm. and by the following May are about 10 mm. long and ready to emerge. It appears that practically all the growth occurs during the winter. The life cycle is completed in one year.

Choroterpes basalis (Banks)

Choroterpes basalis imagoes were collected only in the vicinity of Hook Point. In this one place they are abundant, but considering the lake as a whole, representatives of this species may be cited as relatively scarce. The period of emergence occurs from the end of July to early September. Under aquarium conditions subimagoes almost invariably emerge in the early evening and imagoes on the following early morning, thus, the length of the subimago period is approximately 12 hours. Small groups of males were observed swarming only in mid-afternoon 3–5 meters above the water. Their flight was of the hovering and darting type.

During the course of four summers' collecting only two nymphs were taken outside the Hook Point situation. The nymphs are, however, abundant at Hook Point. Even here they are restricted to a relatively small area where they

occur under old logs and wood fragments which rest on the marl-covered bottom. The distribution of the nymphs ends abruptly along the line where the marl stops and the almost pure sand bottom begins. On one side of this artificial line nymphs are common while on the other side not a specimen can be found. The nymphs react negatively to light and remain under wood during the day coming out on top only at night. They feed on marl and the encrusting organisms found on the wood. When fed similar materials scraped off rocks from Grapevine Point they also ate it just as readily, although they do not occur in that type of habitat. *C. basalis* nymphs were found in other lakes near Douglas Lake but always in the same type of habitat characterized by collections of woody debris.

The life cycle of this species is completed in one year. Collections of nymphs seem to indicate that the eggs overwinter and hatch in late spring or early summer. No very small nymphs of this species were collected although nymphs about one-fourth to one-half grown were taken during July and early August. However, *C. basalis* nymphs were absent from all collections made in October and also from those made in May and June.

Baetisca obesa (Say)

During the four seasons over which collections were made only two male imagoes and two very immature nymphs of *Baetisca obesa* were taken. The adults were collected in flight on the evening of June 18 and the nymphs in mid-September.

Ephemerella bicolor Clemens

Ephemerella bicolor is a very common species emerging in early summer between June 5 and July 10 with a maximum abundance during the latter part of June. Swarming of males takes place along the edge of the lake in the evening about 8:00–8:30 p.m. The length of the subimago period is normally about 24 hours.

The nymphs of *E. bicolor* are numerous in the spring along the open shores on rocks, old wood, and stems of last year's growth of *Scirpus americanus*. No specimens were collected in quiet water situations such as prevail at Hook Point, Marl Bay, Maple Bay, or Sedge Point pools. When ready to emerge, the nymphs migrate shoreward, climb out of the water, and molt just above the water line of an exposed rock at the shore line. They do not seem to be able to emerge from the open-water surface. When mature nymphs were placed in water without a stone or other object on which they could climb out of the water to emerge, they soon died without emerging. However, if a stone, placed in the dish, projected slightly from the water, the nymphs emerged successfully.

The life cycle of *E. bicolor* is completed in one year. Eggs deposited in early summer hatch in late summer or early fall. Recently hatched *Ephemerella* nymphs begin to make their appearance in the lake during the last half of August. At that time the writer found it impossible to specifically identify these very young nymphs since three closely allied species of *Ephemerella* belonging to the *bicolor* group occur in Douglas Lake and certain phases of the life and seasonal cycles of these three species run parallel to one another. However, by October characters appear in the developing nymphs by means of which *E. bicolor* can be separated from the other two species. Practically all of the growth of *E. bicolor* nymphs occurs in the spring after the ice cover disappears. In mid-October the nymphs average about 2 mm. in length and in early May are only around 3 mm. long. The average size of mature nymphs is 7 mm.

Ephemerella lutulenta Clemens

Ephemerella lutulenta imagoes are rather common during the last of May and early June. This species is not as abundant as the other two species of this genus in Douglas Lake. Emergence begins about May 15 and ends about June 10. Swarming activities were not observed.

The nymphs are found close to shore in almost all parts of the lake in the early spring but seem to prefer those areas in which debris collects; they are commonly found on the old stems of *Scirpus*. They do not occur on the open bottoms but under rocks, wood, or other objects to which they cling.

The life cycle is completed in one year. Eggs which are laid in late spring incubate through the summer and probably hatch in late summer or early fall. The small nymphs of *E. lutulenta* and *Ephemerella temporalis* found in the fall probably hatch from eggs at about the same time and although collections made in mid-October seem to contain both of these species, the writer does not feel sure of his ability to distinguish them. In fall collections taken at Hook Point where *E. bicolor* does not occur, there seem to be two sizes of nymphs present, the larger of which may be *E. lutulenta* and the other *E. temporalis*. However, the size groups are not distinct and graduate into each other so as to make impossible positive separation of the two species on this basis alone. Neither can they be separated on the basis of distribution since they occur together in the same situations. Nevertheless, by early May, *E. lutulenta* is readily separable from *E. temporalis* on the basis of size alone for at this time the nymphs of *E. lutulenta* are practically full grown and ready to emerge while those of *E. temporalis* are but little larger than they were in the autumn. Thus, *E. lutulenta* seems to continue its growth throughout

the winter and is the first of the three *Ephemerella* to emerge in the spring.

Ephemerella temporalis McDunnough

Ephemerella temporalis is a very common species and compares equally with *E. bicolor* in relative abundance. The period of emergence is from about June 5 to July 15. It appears to last a few days longer than *E. bicolor* although this may be an apparent rather than an actual difference and may vary from year to year. No swarms of *E. temporalis* were observed although imagoes were readily collected resting on vegtation along the shore. The length of the subimago period is about 24 hours.

In the spring the nymphs of *E. temporalis* are found almost everywhere along the shore in shallow water where old wood, stones, debris, or old culms of *Scirpus* occur. They are more numerous in situations such as Hook Point or Sedge Point pools. In the latter situation, however, they occur only in that pool which is permanently connected with the lake and were not found in the second pool. On Grapevine Point or Fairy Island they are not as abundant as *E. bicolor*. In a quiet situation this species has been observed to emerge from the open-water surface.

As in the other two species of *Ephemerella* that occur in Douglas Lake, this species completes its life cycle in one year. However, there appears to be very little growth of the nymphs during the winter months since collections made in early May contain specimens only about one-half grown. Most of the growth takes place in the spring during the first month after the disappearance of the ice cover.

Tricorythodes allectus (Needham)

Only imagoes of *Tricorythodes allectus* were collected at Douglas Lake. From a small group in swarm about 10:00 a.m. on July 26 at Hook Point three males and three females were taken. On July 29 between 9:00 and 10:00 a.m. a much larger number of specimens was observed swarming over the water along the shore of North Fishtail Bay in the area north of Hook Point and 19 males and 12 females were collected. No nymphal exuviae could be found either at the water's edge or out from the shore on the water surface. No nymphs were collected.

Brachycercus lacustris (Needham)

Adults of *Brachycercus lacustris* were collected in late July. However, collections of nymphs indicate that the emergence period extends well into August and probably early September. No swarms were seen but specimens were reared from nymphs and some nymphal exuviae were found floating on the water surface near the shore line in the early morning. This is a relatively rare species in Douglas Lake.

Nymphs were collected only at depths of 1–3 meters on marly sand bottoms during July and August from Grapevine Point, Hook Point, Big Shoal, Fairy Island, and Marl Bay. *B. lacustris* evidently has a one-year life cycle. It seems probable that the eggs laid in late summer overwinter and hatch in the late spring since only half-grown nymphs were collected in early July and none were found in the autumn or early spring. The emergence period is relatively long and occurs simultaneously with that of *Choroterpes basalis*.

Caenis simulans McDunnough

Caenis simulans is abundant at Douglas Lake and imagoes were collected on various dates throughout most of the summer. The earliest date of adult collections was June 10 and the latest August 11, although a few mature nymphs were collected later which probably would have emerged during the last half of August. The peak of abundance is reached during the last half of June.

Emergence from the nymph, casting of subimago skin, swarming, and mating all occur in the same evening. Toward the end of June the subimago emerges about 7:00 p.m. from the surface of the water, where it leaves the nymphal skin, and alights on the nearest object it contacts, usually the vegetation fringing the lake shore. Molting occurs very shortly thereafter and the first small swarms of males are observed forming between 8:00 and 8:15 p.m. and by 8:30 p.m. dense groups are seen.

During swarming observations of *C. simulans* at Douglas Lake the writer noticed many specimens flying with exuviae fastened to the long tails or tip of the abdomen and trailing out behind as the insect flew. This led to the conclusion that the mayfly might be shedding its exoskeleton during flight. Close observations were made in an effort to see the early part of the process which would consist of molting the exuviae covering the head and thorax. If shedding of the exoskeleton during flight were possible, individuals should have been seen falling through the air during the process as flight would seem to be impossible during such a time. This falling of individuals was not observed. Later it was found that with subimagoes reared in captivity and those observed directly in the field resting on vegetation, exuviation took from forty-five to sixty seconds for completion. This time interval was observed repeatedly. The process was, however, sometimes incomplete to various degrees. Some exuviating specimens even began flight immediately following extrication of the head, thorax, legs, and only a portion

of the abdomen thus carrying the partially shed skin along with them, and giving the impression that molting might have occurred during flight. Burks (1953) states positively that he has observed *C. simulans* shedding the subimaginal skin during flight. On the other hand Berner (1950) observed that *Caenis diminuta* in Florida molted while at rest. Further studies might well be carried on to clarify this subject of exuviation in flight.

Swarms of *C. simulans* males were particularly abundant just at dusk in the evening during late June. Swarming began with small numbers of individuals flying in little individual groups along the lake shore. Gradually as flying individuals became more numerous these smaller groups merged to form larger ones until finally only one or two large, compact swarms were seen in the immediate vicinity where before there had been a number of much smaller ones. Each group was composed of thousands of individuals and formed a dense flying mass 3–5 meters in diameter and 7–10 meters above the water surface. The wings of each individual beat continuously as it darted here and there between other members of the swarm. The members of the swarm faced into the wind and the entire group acting as a unit wove back and forth or up and down seemingly with the changing air currents. Swarming continued until dark after which time observations were impracticable. Both males and females of *C. simulams* were attracted in large numbers to strong lights at night during the height of an emergence period.

Nymphs were abundant at Sedge Point pools and Hook Point cove and common on the organic detritus bottoms of Marl Bay and Maple Bay coves. They were also common in the open lake at depths of 1–3 meters around the littoral zone of most of the lake wherever flocculent marl and organic detritus accumulate. Specimens were collected from the submerged plant zone where they occur both on the plants and the bottom. In the spring and autumn the nymphs are more widely distributed and some specimens were taken in less than 1 meter of water, usually under stones, in various parts of the lake subject to strong wave action such as Grapevine Point and Stony Point. But during the summer these nymphs were very rarely found in water less than 1 meter deep except in very protected situations. Indications are that the life cycle of *C. simulans* in Douglas Lake is completed in one year. Collections taken during May, June, and early July show a preponderance of mature nymphs in the lake. This is correlated with the principal emergence which occurs in June. During the last of July and early August many very young nymphs begin to appear in collections although mature nymphs are still present but in fewer numbers. In late August and early September only an occasional mature nymph was taken but young nymphs were very abundant.

Callibaetis ferrugineus (Walsh)

Callibaetis ferrugineus is a relatively rare species at Douglas Lake and but few specimens were collected during the four seasons. The only adult specimen taken was a female imago but a single male was reared. Nymphs were captured, usually only one or two to a collection, in such places as Sedge Point pools, Hook Point, Marl Bay, and Maple Bay on various dates throughout the summer. Nymphs were never taken along the wave-swept shores of the lake but only in extremely well-protected situations which approach ponded conditions.

Baetis phoebus McDunnough

Adults of *Baetis phoebus* are very common during the entire summer where they were collected resting in vegetation along rocky wave-swept shores. Swarming of this species was not observed. Subimagoes usualy emerge during the afternoon by crawling just out of the water on a partially submerged stone at the shore line. The length of the subimago period is about 24 hours. There appears to be no definite period or periods of emergence except that of the whole summer since adults or mature nymphs were collected at all times between June 10 and October 20. However, mature nymphs and adults were most abundant during July.

The nymphs of *B. phoebus* were found generally distributed along the wave-washed shores of the lake wherever stones occurred at the shore line. They were very abundant on Grapevine Point and as many as 50–60 nymphs of all sizes were often found occupying an area of approximately 5 square cm. under a small stone. Depth distribution of these nymphs is very limited. Most of the specimens occurred on the sides or under partially exposed stones at the shore line and lakeward to a depth of about 15 cm. Very rarely were nymphs collected at depths of 15–30 cm.

Centroptilum fragile McDunnough

Centroptilum fragile was collected only as the adult. Approximately 80 specimens were taken in the course of four seasons, the majority of which were females. Specimens were captured either flying over the water near the shore about 6:00–7:00 p.m. or resting on vegetation. Several subimagoes were collected. The species was most abundant during mid-July; however, specimens were taken from the last of June to mid-August. Swarming seems to occur in late afternoon and early evening. About 7:30 p.m. on July 18, numerous females were seen flying

up from the vegetation along the shore of South Fishtail Bay and ovipositing in the water over a submerged plant zone. No individuals were seen depositing eggs close to the shore which is wave-swept and sandy but only over the deeper water 45–60 meters lakeward from the shore line. Nymphs of this species were not found. Since they occur nowhere else in the lake, it is concluded they are probably restricted to the submerged plant zone.

Pseudocloeon dubium (Walsh)

Only subimagoes and imagoes of *Pseudocloeon dubium* were collected. A total of 16 specimens (10 males; 6 females) were taken on the following dates: July 1; August 8; August 18. On July 1, 10 males and 1 female were captured swarming at 7:30 p.m. along the shore of South Fishtail Bay. The nymphs may be inhabitors of the submerged plant zone since no specimens were found in any of the other habitats.

Cloeon rubropictum McDunnough

Adults of *Cloeon rubropictum* are rather common throughout the summer around Douglas Lake. Numerous imagoes were reared or collected from vegetation along the shore. Swarming usually occurred about 7:30 p.m. during mid-summer. The emergence period appears to be an extended one and lasts from about June 15 to October 15. Imagoes were most abundant between the last of June and the forepart of August.

Nymphs of *C. rubropictum* were found generally distributed around the entire littoral region of the lake at a depth of about 0.5–1.0 meter. They were most numerous on the top surface of marl encrusted rocks and rarely found on clean rocks of open bottom.

SUMMARY

Information obtained during a four-season investigation is presented on seasonal distribution and life cycles of 22 species of Ephemeroptera known to occur in Douglas Lake, Cheboygan County, Michigan. Data are given on the relative abundance of adults including total length of emergence period, time of maximum population density, and length of the subimago stage. Swarming activities of a number of species are discussed. A trimodal seasonal emergence of three separate broods, each with a cycle of one year, is postulated for *Stenonema femoratum* and *S. interpunctatum*. The relative length of the incubation period of the eggs of various species based upon field observations under natural conditions is given. Also discussed are the seasonal differences in growth rate of nymphs. The littoral distribution and the type of habitat occupied by the different species of nymphs are reported. A life cycle of one year is typical for most species of mayflies in Douglas Lake; however, *Hexagenia limbata* requires two years to complete its development.

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NEORHYNCHOCEPHALUS SACKENII AND TRICHOPSIDEA CLAUSA, NEMESTRINID PARASITES OF GRASSHOPPERS[1]

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In 1949 and 1950 two nemestrinids, *Neorhynchocephalus sackenii* (Will.) and *Trichopsidea clausa* (O.S.), were frequently encountered parasitizing grasshoppers in the range-grass areas of Montana. Although these species belong to separate subfamilies, their general appearance, behavior, and life cycle are strikingly similar. The adult of *sackenii* is readily distinguished from that of *clausa* by its elongate proboscis as well as by its generally smaller size. The proboscis of *clausa* is represented by a rudimentary stub only. The females of both species have a slender almost filiform, upcurved ovipositor, adapted for feeling the way into crevices rather than for piercing.

Although nemestrinid flies have been collected and catalogued over a considerable period of time, surprisingly little has been published concerning their biology and habits. *N. sackenii* and *T. clausa* had previously been encountered by Spencer (1931) in British Columbia. In 1929 he found *clausa* (then mistakenly identified as *Rhynchocephalus sackenii*) near Riske Creek in Cariboo Province, and assumed that it had been parasitizing woodboring beetles. In 1943 he reported finding *sackenii* on cattle ranges near Kamloops and mentioned rearing *clausa* from the grasshopper *Camnula pellucida* (Scudd.) and *sackenii* from *Melanoplus mexicanus mexicanus* (Sauss.) (Spencer 1945). Bequaert (1950) reported that the first rearing of *clausa* in the United States to come to his notice was by R. E. Pfadt in 1942 from the grasshopper *Metator pardalinus* (Sauss.).

The two nemestrinid species encountered in Montana are of special interest because the larvae were heavily parasitizing some grasshopper species with evident damage to their reproductive organs. The 1949–50 studies (York and Prescott 1952) dealt largely with *clausa* because of its unusual abundance in some grasshopper areas being worked during these two seasons. This situation was reversed during the summer of 1951, when *sackenii* was the more abundant parasite in the particular areas visited, and consequently became the major source of the material on which the present study is based.

This study was made in response to a need for information on these little-known parasites, especially such information as would make possible an evaluation of their importance in the suppression of grasshopper populations. It deals with matters of their behavior, life history, differences in structure and mode of parasitization, host preferences, and effect of parasitization on host reproductive capacity.

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GENERAL OBSERVATIONS IN MONTANA

During the summer of 1951 the author made observations on *sackenii* in the Cottonwood area 7 miles north of Bozeman, in Gallatin County, Montana. This area, drained by Cottonwood Creek, lies close to the west base of the Bridger Mountain range. Over a series of seasons it harbored high grasshopper populations in which *Melanoplus mexicanus* (Sauss.) was dominant. Cultivated fields devoted chiefly to the production of small grains are intermixed with small fenced-in remnants of original range and pasture acreage. Because of the high elevation (about 4,800 feet) and proximity to the mountain range, grasshopper development is normally several weeks behind that in the typical plains areas of eastern Montana.

Parasitization of grasshoppers by *sackenii* in this area was first noted in the fall of 1950, when about 2 percent of *Melanoplus mexicanus*, *M. dawsoni* (Scudd.), and *Encoptalophus sordidus* (Scudd.) contained larvae of this nemestrinid. A few of these larvae were successfully reared and their identity determined.[3] In July 1951 not only could the adult flies be found in the immediate Cottonwood vicinity where most of the observations were made, but inspection of fence posts, where the females gathered to oviposit in wood beetle holes, revealed their presence in most of the general area lying at the west base of the Bridger Range for a distance of 15 miles. *Trichopsidae clausa* was not encountered in this area.

The first visits to the Cottonwood area in 1951 were too early and subsequent visits too late to catch the first emergence of *sackenii* flies. The flies were first noted in that season when the area was visited on July 17. Other visits followed on July 18, 21, 24, 25, 26, 30, August 1, and on several subsequent dates extending into mid-October, when grasshoppers began to succumb to age and frosts.

All the July visits to the area were timed so that arrival was before 9 a.m. Observation had shown that no nemestrinid flies were active or

[3]Determination by W. W. Wirth, Division of Insect Detection and Identification, Entomology Research Branch, U. S. D. A.

anywhere in evidence before this hour, even though the sun would be rather high and the air sufficiently warm to induce activity in bee flies, asilid flies, and sarcophagid flies. The buzzing of the nemestrinids could be heard and the flies seen in the grass beginning about 9:30, by which time the air temperature had risen to approximately 72° F. and the ground temperature to around 108°. Almost another hour elapsed before the female flies appeared on the fence posts to oviposit in the beetle holes. By noon the number of flies in the grass had greatly diminished, although they were approaching maximum numbers on the posts. By mid-afternoon the number on the posts had gradually declined, and by 5 p.m. only an occasional individual could be found.

The movement of the flies in the morning from the grass to the posts was often observed. During this period the flies would frequently be seen buzzing along the lower strands of barbed wire

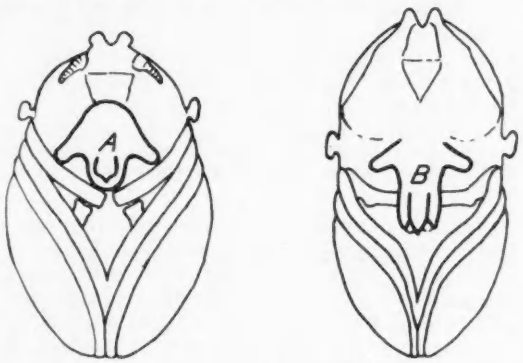

FIG. 1. Ventral aspect of pupal head and thorax of *Trichopsidea clausa* (left) and *Neorhynchoephalus sackenii* (right). Differences in the impression of the proboscis and associated structures are evident in the heavily outlined areas A and B. (Drawings made from empty pupal shells.)

just above grass level, probing the seams in the twisted wire with their ovipositors in an attempt to find favorable oviposition sites. Within an hour or so most of them would have found satisfactory fence posts with beetle holes and settled down to the task of laying eggs in these cavities.

On the first three visits (July 17, 18, and 21) the flies were at their maximum seasonal abundance, and in the morning could be found in the grass at the rate of two or three per minute of searching. They were first detected by the sound of their buzzing wings and later seen by following the source of the sound with the eye.

Pupal shells could be found in the area where the flies were most abundant in the grass. They were usually within an inch or two of the holes through which the pupae had come to the soil surface. The pupal shells of *sackenii* were readily distinguishable from those of *clausa*, collected in other areas, by the more elongate impression of the proboscis. This impression, shown in figure 1, is a low, blunt excrescence on the facial surface of the pupa. Other differences in the immediate area of the proboscis are also evident.

In selecting fence posts for oviposition, the flies favored those that had an abundance of beetle holes of suitable size. Posts with small shot-hole borer tunnels were of little attraction, whereas holes about ⅛ inch in diameter were preferred. *N. sackenii* was not observed to oviposit in weather checks of posts—a common habit of *clausa*.

Even at peak numbers (between July 17 and 21) the flies were never abundant on the fence posts. One fly to every two or three posts was average, although three or four flies could frequently be counted on certain favored posts. Nine were the most ever counted on a single post. In contrast, occasionally eighty or more *clausa* flies were found on a single post on the Golder area in 1950 (York and Prescott 1952).

July 17 was the first date on which *sackenii* flies were observed to emerge, although there probably had been some emergence a few days before. However, the comparatively few beetle holes that contained nemestrinid eggs and the fresh appearance of eggs found on this date indicated the beginning of emergence. This date was over five weeks later than the 1951 peak of emergence of *sackenii* and *clausa* adults in southeastern Montana. However, development of the host grasshopper species at the time of peak emergence of the flies was nearly the same in both areas, the majority of grasshoppers being in the second and third instars. *Melanoplus mexicanus*, because of its great numerical dominance at the time of *sackenii* larval activity, was the principal, although not the preferred, host in the area.

Sexual activity was not observed in either species. Males were never seen on or around fence posts where females gathered to oviposit. Where both sexes were found close together in grass, they appeared oblivious to one another's presence. Yet Bequaert (1934) reported another member of this genus, *Neorhynchocephalus volaticus* (Will.), as "rather frequently seen mating."

An interesting relationship in this connection was the great preponderance of female flies in morning counts taken in the grass on successive dates. On July 17, after a dozen or so flies had been checked, no males were encountered. On July 18, of 18 flies counted on the grass, 17 were females; on July 21, 11 of 18 were females; and on July 24, all of 6 were females. Thus, for a total of 42 flies counted on the grass during three days, 81 percent were females.

The great preponderance of females came as a surprise, since a reverse condition had apparently existed in 1950 with respect to *clausa* in the

Golder area. Although the females of that species had been found ovipositing in phenomenally large numbers, fully 90 percent of the flies collected on the grass were males. A possible explanation of this situation in the Golder area is that the principal emergence of *clausa* flies apparently takes place in the morning after the sun has warmed the soil, whereas most of the observations were made in the afternoon, when most of the females had probably gone to the posts to oviposit. It seems possible from their great number on the posts that females might have outnumbered the males in the Golder area also had morning counts been made in the grass at the time the flies were emerging.

Another interesting fact is that neither species was ever observed feeding under natural conditions, although flower heads in the areas studied were frequently checked. Bequaert (1934) made the following references to *Neorhynchocephalus* spp. feeding on flowers:

(1) "Professor R. H. Painter writes me that, in Kansas, he found most of his specimens (*N. volaticus*) hovering among fairly tall grass. On one occasion, in Pottawatomie Co., Kansas, a number were feeding at flowers of *Houstonia*."

(1) "Most of the *N. sackenii* and *N. volaticus* were taken by him [R. H. Beamer] in meadows while hovering over flowers. * * * the only published flower record I can find is that by Robertson [1928, Flowers and Insects, p. 47.], who took *N. sackenii* from *Achillea millefolium*, at Carlinville, Illinois."

The long, needle-like proboscis of *sackenii* suggests an adaptation for feeding on the nectar of flowers. Although the necessity of either *clausa* or *sackenii* for feeding in the adult stage has not been entirely evident in view of their apparent short life span and oviposition period, there seems to be no question as to the ability of *sackenii* to feed. Adults kept in glass containers at room temperature for 12 to 14 hours did not respond when offered small water-saturated cotton balls. However, when similar pellets were saturated with sugar solution, the flies immediately lapped it up, and there seemed no doubt that their mouth parts were functional. No *clausa* flies were available for similar tests.

From peak numbers between July 17 and 21, *sackenii* flies began a rapid decline, which was first evident in the visit on July 25. A check made on July 26 between 10:35 and 11:20 a.m., in weather that was calm, clear, and warm, revealed only five flies on 56 posts and only one fly in the grass. Although this date marked the end of substantial fly populations in this area for the season, an occasional straggler was found on posts as late as August 13.

LARVAE IN THE FREE STATE

The first free larvae of *sackenii* were observed on fence posts on July 31, although examination indicated that there had been some hatching for a week or ten days. The larvae were constantly on the move, crawling into and out of crevices and holes on the post. In relation to the number of eggs that ultimately showed evidence of having hatched (the numbers running into the thousands), larvae on the posts were very few. Many posts on which oviposition had been fairly heavy were examined before one could be found with larvae on it. Usually such larvae were confined to one or two small areas of a few square inches, and it was not possible to count more than 10 to 30 at any one time.

Some observers have assumed that the free larvae depend upon wind as their means of dispersal over areas occupied by the host. (This assumption may be based partially upon the known habits of other species of Nemestrinidae.) The tendency of the flies to seek elevated objects upon which to oviposit seems to accord with this idea. In discussing the nemestrinid *Hirmoneura obscura* Meig., Williston (1908, p. 186) described the behavior of the larvae as follows:

"These larvae issued in great numbers from burrows (in the pine rails of fences) in which they were hatched and, placing themselves erect, were blown away by the wind."

There is no doubt that nemestrinid first-instar larvae, if cast into the wind, could be blown for a considerable distance. Difficulty was frequently encountered in 1950 when attempts were made to collect *clausa* eggs from crevices in fence posts. As the eggs were being removed, the mildest breeze frequently blew them away. The 1949–51 observations on both *sackenii* and *clausa* revealed the following facts of interest in this connection:

(1) Although the flies seek elevated objects such as posts, poles, and trees upon which to oviposit, they do not necessarily seek the highest portions of such objects. Where there was ample choice, flies were noted ovipositing at any point in an elevation range from 3 to 40 feet.

(2) Although oviposition was so heavy on fence posts that every beetle hole was crammed full of eggs, numbering into thousands to every post, at hatching time usually only a few larvae were found on the outside of the posts.

(3) The larvae that could be seen were incessantly on the move, crawling in every direction. Yet there was no tendency to crawl to, or gather upon, the upper areas of the posts.

These observations of larval behavior, when compared with that of *Hirmoneura obscura* as described above by Williston, suggest the possibility of some differences between species in behavior relating to dispersion.

Some observations were made of the behavior of newly hatched *sackenii* larvae under windy

conditions in the Cottonwood area. On August 1 a wind developed from thunder clouds while from 20 to 30 larvae under observation on a fence post were occupying an area about 2 inches in diameter. The wind was rather gusty, so that the effect of many different velocities on the larvae could be observed. It was estimated that gusts attained a maximum velocity of about 25 m.p.h. All the larvae were crawling and showed no tendency to stand on end as specimens in the laboratory had been seen to do. As the wind gathered in strength, the larvae were sometimes buffeted from side to side, but they usually succeeded in holding on. Occasionally two or three would be simultaneously blown away. It was repeatedly noted that grasshoppers collected close to the *sackenii* oviposition sites (less than 30 feet) showed a much higher parasitization than those collected farther away, although no data were obtained.

Lack of time and facilities prevented the detailed study upon which an adequate description of the first-instar larva should be based. Field observations with a binocular microscope showed it to be similar to the first-instar larva of *clausa* in both appearance and behavior. Figure 2 shows sketches of a *clausa* first-instar larva made in southeastern Montana in 1950. This larva is similar to the first-instar larva of the nemestrinid *obscura* as illustrated by Handlirsch (1883) and copied by Clausen (1940). The spines upon the "pseudopods" of the abdominal segments of the *clausa* larva appear to be without hooks, however, and the fleshy processes on the last abdominal segment number six instead of four, and are much longer, more filiform, and terminate in what appears to be either a small suction disc or an adhesive pad.

The larva crawls rapidly with a typical caterpillar-like undulation of the body, using the six long, fleshy processes constantly, seemingly to assist in clinging to surfaces. As the larva in forward motion moves away, the disc-like terminal processes are brought ahead in rhythmic repetition and planted firmly upon the substratum. This is accomplished by an upward bowing of the six filamentous processes, which are again instantly straightened out. Captive larvae placed upon grasshoppers, or in other situations, were noted frequently to stand upright upon the posterior end, sometimes "frozen" in a statuesque attitude for prolonged intervals and sometimes waving their bodies about in the typical blind groping behavior characteristic of many caterpillars.

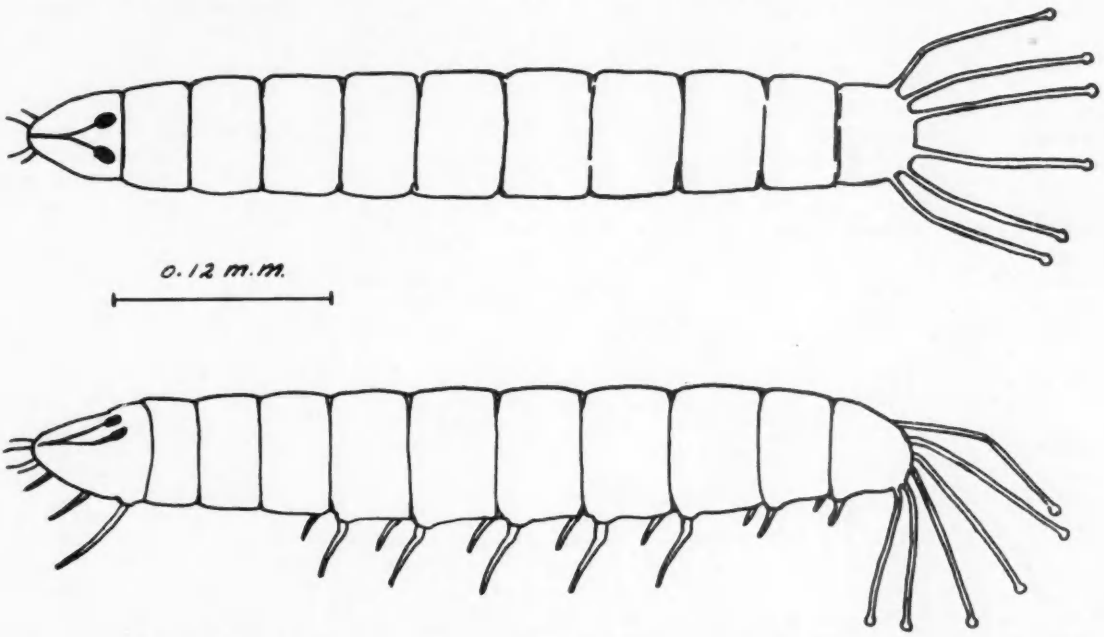

FIG. 2. Dorsal (above) and lateral (below) aspects, first-instar larva of *Trichopsidea clausa* in the free state.

LARVAL PENETRATION OF HOSTS

On July 31, one week after evidence of hatching had been observed in *sackenii* eggs on fence posts, the first successful effort was made to find evidence of parasitization by the larvae in grasshoppers. Because of the minute size of very young larvae, none were found in the hosts by this date, but

larva penetration marks were found in abdominal segments of a few of the grasshoppers. In checking grasshoppers in the field for parasitization, the method first employed was to remove the head from the grasshopper, squeeze the abdomen between the thumb and the forefinger until the body contents were ejected from the anterior end of the thorax, and then examine these for nemestrinid larvae. This method, although admittedly crude, probably revealed most larvae after they had attained a length of 6 or 7 mm., but it certainly failed to reveal all the smaller larvae. However, in 1951 it was found that a dark spot on the exterior ventral area of the abdominal wall of the grasshopper clearly marked the point where the invading larva had penetrated, as well as the point where the parasite's respiratory tube connected with the host's integument to form its vent to the exterior. These penetration marks are characteristic and easily recognized. Their typical location on the abdominal segments is well shown in figure 3. Multiple penetration marks, indicating penetration by several larvae, were very common in all the grasshopper species attacked.

The penetration mark is in reality the terminal portion of the opaque dark-brown respiratory tube showing through the transparent integument of the host plus a certain discoloration of the host's tissue due to injury. The respiratory vent (not distinguishable in the photograph) is situated at the posterior end of the mark, which, following the progress of the invading larva, usually leads upward and forward toward the adjacent spiracle, as shown in figure 3. This rather pronounced spiracular orientation in *sackenii* larvae was not accounted for, since no connection of the larval respiratory tube with the host's spiracles or associated tracheae was found in many grasshoppers examined.

The abdominal area of the host to which *sackenii* larval punctures are limited seems to be related to the method by which the larva finds its way to the precise locus of penetration, slightly below and posterior to a spiracle. This site appears to be reached almost automatically as a result of the tendency of the larva, upon contacting the host, to work its way beneath the soft intersegmental folds of the abdominal venter. From this location the larva is guided more or less by the inner contour of the fold to the point where penetration is made. No condition similar to this is provided by the hard sclerotized plates composing the thoracic venter, or by the first abdominal segment, which is drastically modified to effect juncture with the thorax and to accommodate the tympana.

Where dissection alone was used, even with the aid of binoculars, it was almost impossible to detect parasitization in its early stages, because of the minuteness of the nemestrinid larvae and the similarity of their coloration to that of the host's tissues. The penetration marks, however, pin-pointed the exact position of the larva, or the point of attachment of its respiratory tube. The marks likewise afforded an accurate and rapid method of separating parasitized from nonparasitized grasshoppers.

Although *sackenii* and *clausa* were the only nemestrinid parasites of grasshoppers encountered in Montana, both species were in evidence in most rangeland locations where nemestrinids were found. Under these circumstances it had heretofore been impossible to tell upon inspection of the hosts which species was involved. The 1949–50 studies had revealed that *clausa* larvae produced no penetration marks upon their hosts. The discovery of the penetration marks of *sackenii* larvae in 1951 therefore afforded an instant and convenient means for determining which species of parasite was infesting grasshoppers being examined.

A search for the reason why *clausa* larvae produced no penetration marks upon their hosts revealed some interesting differences in the habits of the two parasites. It was found that *clausa* larvae, unlike *sackenii* larvae, gain entry to their hosts by puncturing the tracheae just inside the hosts' spiracles. From this it seems a fair presumption that they gain access to the tracheae through the spiracles. In this connection it was noted that penetration was confined exclusively to the tracheae of the large spiracles of the thorax and, more often, of the first abdominal segment. It was with these tracheae that the *clausa* respiratory tubes always made junction. The abdominal segments, with the exception of the first, have spiracles entirely too small to permit free entry of nemestrinid larvae.

A remarkable parallel to this distinction between the respiratory arrangements of the two nemestrinid species is found in two tachinid parasites described by Clausen (1940). In his illustration the larva of *Prosena siberita* (F.) is shown with its respiratory tube attached to the host's trachea near a spiracle, and the larva of *Dexilla ventralis* (Ald.) with its respiratory tube attached to a puncture in the host's skin through which the first-instar larva had entered.

These different requirements of *sackenii* and *clausa* larvae for gaining entry to their hosts have resulted in a sharp line of division between the body areas of the host which each parasite penetrates and to which each attaches its respiratory tube (figure 3).

RESPIRATORY TUBES OF LARVAE

The larvae of *sackenii* and *clausa* within the host, once they reached 6 mm. in length, could be distinguished readily by a marked difference in their respiratory tubes. Variations from the 7 mm. average length of fully developed *sackenii* tubes rarely exceeded 2 mm. However, fully

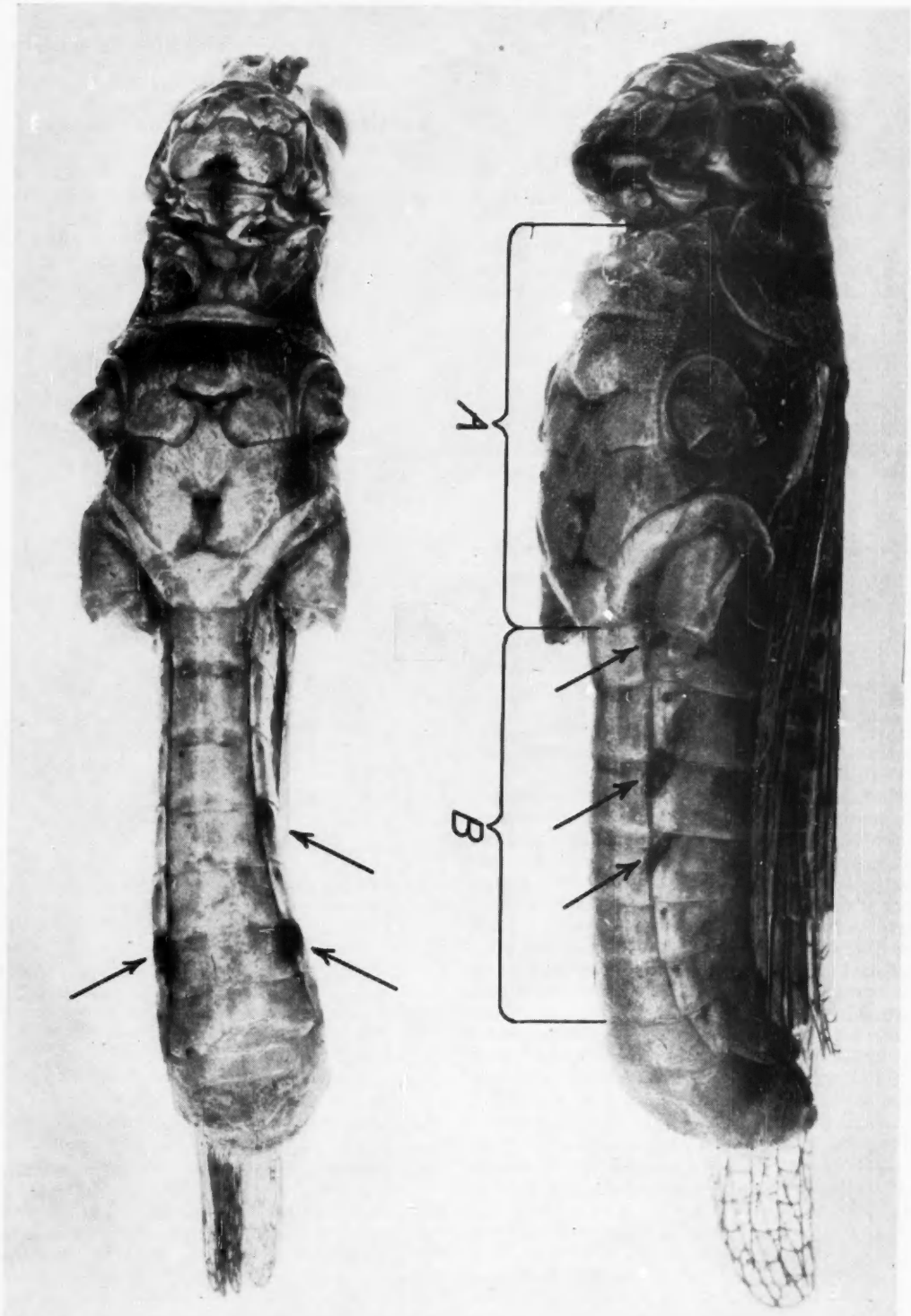

FIG. 3. Lateral (above) and ventral (below) aspects of *Melanoplus mexicanus*, with legs removed, showing penetration marks (arrows) made by *Neorhynchocephalus sackenii* larvae. Area of attachment of respiratory tubes of *Trichopsidea clausa* (A) and *sackenii* (B).

developed tubes of *clausa* larvae taken in 1950 from *Metator pardalinus* and *Arphia pseudonietana* (Thom.) averaged slightly over twice as long as those of *sackenii*, and the length corresponded fairly closely to that of the larvae themselves. This much greater length without corresponding increase in diameter gives *clausa* tubes a more sinuous appearance. The tapering from the proximal to the distal end was therefore much more apparent in the tubes of *sackenii* larvae.

The respiratory tubes of *sackenii* and *clausa* larvae are remarkable structures. They are constructed like a coiled spring, the closely appressed spirals of which form a continuous tube. Forced stretching of the tube beyond a certain limit ruptures a membranous sheath connecting the coils and allows them to separate broadly after the manner of a corkscrew.

The fully developed respiratory structure consists essentially of the respiratory tube modified at the distal end (figure 4) to form attachment

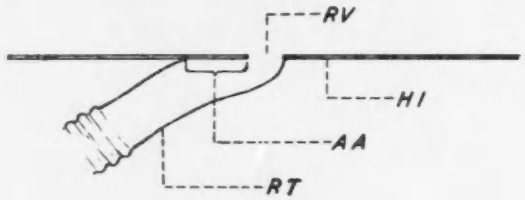

FIG. 4. Terminal portion of respiratory tube of *Neorhynchocephalus sackenii* larva at point of attachment to host's body wall. *AA*, anchor area; *HI*, host's integument; *RT*, respiratory tube; *RV*, respiratory vent.

and outlet to the body wall of the host and at the proximal end (figure 5) to form attachment to the larva itself. A portion of the distal end adjacent to the respiratory vent is attached firmly, as though grafted, to the host's integument at the anchor area (*AA*). The extreme distal section has a smooth exterior, which shortly gives way to the transversely corrugated effect produced by the spiral coils constituting the tube proper. The proximal end of the tube is enormously enlarged to form a respiratory sleeve, which fits snugly over the posterior end of the larva. This sleeve, covering the last three or four larval segments, encloses the two round 19-rayed spiracles of the last segment.

In the immature larva the respiratory sleeve tapers off gradually to form the respiratory tube proper. But as the larva matures that portion of the respiratory sleeve that covers the last abdominal segment bearing the two spiracles becomes a cup-like structure, for convenience designated as the respiratory cup (*RC*).

The main portion of the respiratory sleeve, although too thick to be considered membranous, nevertheless is sufficiently flexible to adjust to any change in the larva's shape resulting from respiratory or other forms of movement. The portion of the sleeve constituting the respiratory cup is somewhat more rigid.

DEVELOPMENT OF LARVAE WITHIN THEIR HOSTS

The first-instar larva of *Neorhynchocephalus sackenii* is about 0.5 mm. long when it first contacts the host. From the second instar on, the larva within the host, with a length-width ratio of about 7:1, is vermiform until it approaches maturity, when it "fattens" rapidly until the

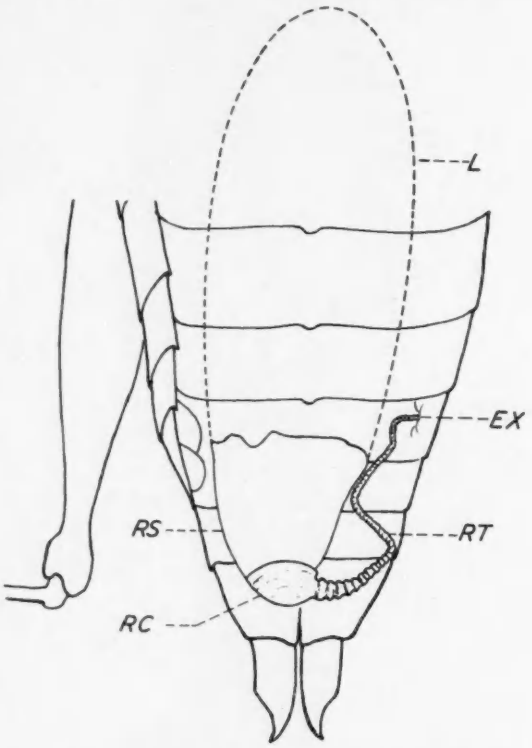

FIG. 5. *Melanoplus mexicanus* dissected to show cast-off respiratory structures of *Neorhynchocephalus sackenii* larva remaining in host after emergence. *EX*, exit of respiratory tube to host's exterior; *RC*, respiratory cup; *RS*, respiratory sleeve; *RT*, respiratory tube; *L* (dotted line), position occupied by larva prior to its emergence.

length-width ratio finally approximates 3:1. The size of the mature larva when it emerges from the host varies with the size and condition of the host. Larvae from *Melanoplus mexicanus* hosts were found to range from 9 to 13 mm. in length, with an average of 11 mm. *Trichopsidea clausa* larvae that emerged from *Metator pardalinus* in southeastern Montana ranged from 12 to 20 mm., with a 13 mm. average. Live mature larvae, in contrast to immature larvae, contract to their minimum length when disturbed. All

the measurements of mature larvae were made in their contracted condition; crawling larvae fully extended are up to 25 percent longer. The full-grown larvae of both nemestrinids are chunky, thick-skinned, and solid to the touch. The segments are encircled by numerous small wart-like excrescenses, (figure 6), which may serve the purpose of traction against the side walls of the tunnel made by the larva when it enters the soil.

Except when they were extremely small, the larvae of both nemestrinid species were always found with the head forward in the host's body cavity. This positional orientation was evident

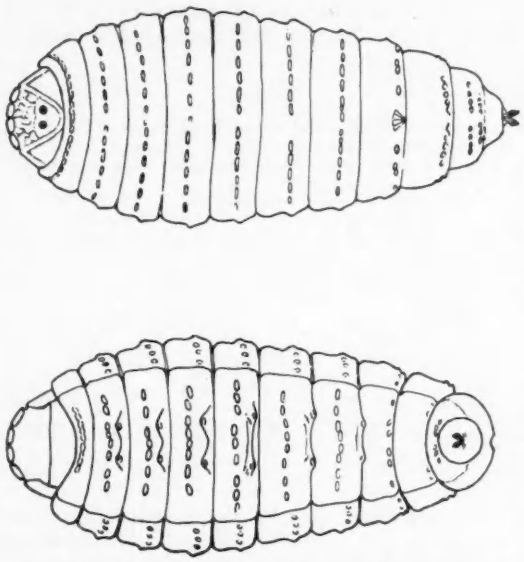

FIG. 6. Dorsal (above) and ventral (below) aspects of mature *Neorhynchocephalus sackenii* larva just after emergence from host, showing the single pair of spiracles on the posterior segment, wart-like excrescences encircling segments, and mouth hooks.

even in the respiratory attachments, shed by the larvae upon emergence from the host (figure 5). They were found by dissection in the extreme lower abdominal region of the latter.

The nemestrinid larvae showed no tolerance toward each other after they had entered the host. The beginnings of several respiratory tubes in hosts bearing several penetration marks were often found in the form of short stumps projecting into the host's body cavity, each stump indicating penetration by one larva. Occasionally a grasshopper containing two living larvae was found, but these larvae were never much over 2 mm. in length. Larger *sackenii* larvae were invariably found singly in their hosts. However, during the 1949–50 observations in southeastern Montana, a host of *clausa* larvae was occasionally found containing both a very small and a very large larva. The large larva was invariably dead, apparently killed by the smaller one.

Just what the lethal principle is and how it operates to destroy all but one of the nemestrinid occupants of a host was not determined. It seems probable, however, that a physical injury is inflicted by one larva upon the other. If, in its random feeding upon tissues within the host, a larva happened to chew through the respiratory tube of another larva, the larva with the punctured tube might succumb from suffocation, since liquids from the host rather than outside air would most likely be drawn into the tube. The large larva occupies a relatively fixed position in the host, with its head projecting almost into the host's thoracic region. The smaller larva, a later arrival, occupies an area near the posterior end of the larger larva. In this position it can do considerable damage to the larger larva by random feeding while itself remaining out of reach of the larger larva's mandibles.

The intolerance of nemestrinid larvae toward one another during their occupancy of the host does not extend to all other species of parasitic larvae. Two grasshoppers were found containing both a large *sackenii* larva and a large sarcophagid larva crowded together in their abdominal cavities.

The extended period of time over which small *sackenii* larvae were encountered in their hosts indicates that they may be able to survive in a free state for a considerable interval after hatching. The larvae encountered in dissected hosts on August 24 ranged from 1 to 7 mm. in length, the majority being less than 4 mm. Fairly small larvae were found in grasshoppers examined as late as September 20; four of them measured 4, 6.5, 7, and 8 mm. in length.

EMERGENCE OF LARVAE FROM THEIR HOSTS

The first emergence of mature *Neorhynchocephalus sackenii* larvae from the hosts was early in September. The developmental stage of larvae in dissected hosts indicated that some may have emerged by September 5. The first observation of emergence was made on September 10 from a grasshopper killed by immersion in ethyl alcohol. Larvae continued to emerge well into October from grasshoppers periodically collected in the Cottonwood area and kept at room temperature in screen cages. As the temperature declined with the advance of the fall season, both the activity of the hosts and the development of the parasites were retarded. By mid-October many larvae succumbed to winter conditions along with their hosts before being sufficiently developed to emerge and find their way into the soil.

The act of emergence of *sackenii* larvae from grasshoppers was frequently observed. In all cases the mature larva made exit through the

soft membranous tissue posterior and adjacent to the point of attachment of the host's hind femur. This had previously been found to be the favorite, though not exclusive, point of emergence of *clausa* larvae (York and Prescott 1952).

Many hosts of *clausa* observed in 1949 and 1950 survived after larval emergence, but emergence of *sackenii* always coincided with the death of the host. However, the emergence itself did not appear to cause the death of the grasshopper. The consumption by the larva of the internal organs of the host seemed to be so well adjusted that the host was enabled to live, take nourishment, and develop normally until the parasite attained appreciable size. By the time the larva reached maturity, however, the host was little more than a moribund shell filled by the parasite. The larva, as if sensing that the host was no longer tenantable and being ready to emerge, made its exit almost simultaneously with the demise of the host.

Emergence was often precipitated by killing the grasshopper with an insecticide or ethyl alcohol. Normally the nemestrinid larva in its host shows very little movement. When the host succumbs, however, the mature larva becomes active in its effort to free itself. The larva is so situated in the host's abdominal cavity that the bellows-like action of the host's abdomen could scarcely fail to cause air to be inhaled and exhaled through the larva's respiratory tube. It is possible, therefore, that respiration of the larva is dependent upon that of the host and that its emergence is precipitated by cessation of respiration of the latter.

The act of emergence usually requires from a half-hour to an hour. The larva, once free from its host, after a brief moment of exploratory crawling, burrows into the soil to a depth of 1 or 2 inches, where it remains throughout the winter and spring. Pupation takes place early in the summer, 2 or 3 weeks before the adults emerge.

GRASSHOPPER COLLECTIONS

Grasshoppers were collected in several fields in the Cottonwood area to determine the species present and the progress of parasitization with relation to host development and seasonal advance. Where comparable data were desired, collecting locations were established, and all the collections made on different dates were taken at the predetermined locations. The sweeps composing each collection ranged from a few feet of the surrounding fence lines to the estimated center of each field—approximately 5 to 400 feet from the posts from which the *sackenii* larvae were dispersed. Such collections were made on July 17 and 31, August 13 and 24, September 7, 17, and 27, and October 5. A few of the records are summarized in the accompanying tables.

TABLE I

SPECIES COMPOSITION, STAGE OF DEVELOPMENT, AND PARASITIZATION OF GRASSHOPPERS AT BEGINNING OF ATTACK BY *Neorhynchocephalus sackenii* LARVAE. GRASSHOPPERS TAKEN ON JULY 31

SPECIES	THIRD INSTARS		FOURTH INSTARS		FIFTH INSTARS		ADULTS		TOTAL	
	Number	Percent Parasitized	Number	Percent Parasitized	Number	Percent Parasitized	Number	Percent Parasitized	Number	Percent Parasitized
Melanoplus mexicanus	208	0	320	0	140	0.7	3	0	671	0.1
Melanoplus dawsoni	1	0	3	0	1	0	0	0	5	0
Camnula pellucida	0	0	0	0	4	0	216	3.7	220	3.6
Aeropedellus clavatus	0	0	0	0	0	0	17	35.0	17	35.0

Table I shows the species composition, developmental stages, and percentage of parasitization of grasshoppers collected when the parasites were beginning their attack. At this time the percentage of parasitized grasshoppers was low in the dominant species and *sackenii* hatching was at its peak. All grasshoppers bearing penetration marks were recorded as parasitized. Striking differences among host species in their incidence of such marks were apparent even at this early stage of parasitic attack, the incidence being highest in those species that hatched and matured first. *Melanoplus mexicanus*, just beginning to come into the adult stage, showed a slight amount of parasitization among the fifth instars. All but a few *Camnula pellucida* grasshoppers had reached the adult stage by this time, and in all collections in which it was represented this species showed a much higher incidence of penetration marks than later-developing species. Even surpassing *pellucida* in this respect was *Aeropedellus clavatus*, which had been in the adult stage so long that the surviving individuals showed signs of aging. This species was the most susceptible to attack by *sackenii* larvae. Our observations had shown that the *sackenii* larvae

were unable to develop within this host after they had entered. Furthermore, even if development were possible, the larvae would succumb before reaching maturity because of the early maturation and death of the host.

The collections indicated that the larvae were entering their hosts only while the latter were in the fourth and fifth instars and the adult stage, the incidence of parasitization increasing with the development of the grasshopper. The larvae apparently were able to penetrate the integument of old adults readily.

From July 31, when the recently hatched *sackenii* larvae began to enter their hosts, there was an increasing incidence of parasitization in *Melanoplus mexicanus* for approximately 24 days. By the end of this time parasitization for all grasshopper species had reached its maximum for the season.

TABLE II

SEASONAL MAXIMUM OF PARASITIZATION BY *Neorhynchocephalus sackenii* LARVAE. GRASSHOPPERS TAKEN ON AUGUST 24.

Species	Fourth Instars		Fifth Instars		Adults		Total	
	Number	Percent Parasitized	Number	Percent Parasitized	Number	Percent Parasitized	Number	Percent Parasitized
Melanoplus mexicanus...	68	4.4	393	6.6	482	10.4	943	8.4
Melanoplus dawsoni.....	0	0	6	0	48	25.0	54	22.2
Camnula pellucida.....	0	0	0	0	8	62.5	8	62.5
Ageneotettix deorum.....	0	0	0	0	6	33.3	6	33.3
Amphitornis coloradus...	0	0	0	0	9	22.2	9	22.2

Table II shows the parasitization at its approximate seasonal maximum. Parasitization of this collection was fairly representative of grasshopper populations in the area. Higher parasitization was found in collections from certain locations. One collection showed 75 *mexicanus* grasshoppers to be 36 percent and 45 *dawsoni* to be 27 percent parasitized.

Some reduction in parasitization was noted after mid-September, probably as a consequence of higher mortality in the parasitized grasshoppers.

HOST PREFERENCE OF NEORHYNCHOCEPHALUS SACKENII

Observations in 1949, 1950, and 1951 have shown *Neorhynchocephalus sackenii* and *Trichopsidea clausa* parasitizing many species of grasshoppers. However, even where both parasites have been found simultaneously in a given location, as was frequently the case, they have never been found parasitizing the same species of grasshopper. Of course, the list of known host species is not yet complete, but enough host species have been determined to suggest a separation of the species that these two nemestrinids parasitize. The determined hosts of *sackenii*, with some exception are smaller than those of *clausa*, which may account for a corresponding difference in the size of the two parasites.

There was no relationship between the intensity of *sackenii* attack upon a grasshopper species and its success in parasitizing the species. If we consider penetration marks as evidence of attack and the presence of developing larvae in the host's body cavity as evidence of successful parasitization, some species of grasshoppers were infrequently or never attacked and never successfully parasitized, some species were heavily attacked but not successfully parasitized, some species were heavily attacked and successfully parasitized, and some were lightly attacked and successfully parasitized (Table III). Thus *Melanoplus mexicanus*, the principal supporting host of the parasite because of its preponderance in the overall grasshopper population, was only lightly attacked but nevertheless successfully parasitized.

EFFECT OF PARASITIZATION BY NEORHYNCHOCEPHALUS SACKENII ON HOST REPRODUCTION

By the time the *Neorhynchocephalus sackenii* larva becomes mature, it has consumed all adipose tissue of the host and reduced a large portion of the host's internal organs and tissues to a shriveled, dehydrated condition. It seems probable that the life of the host is considerably shortened thereby, and it is certain that the reproductive potential is greatly reduced. After the parasitic larva has reached medium length, its head lies within the region occupied by the ovaries and associated egg mass of the host. The larvae then feeds upon these organs and related tissues, finally bringing about their complete destruction.

It seems possible that grasshoppers may lay some eggs during the early stages of parasitization, especially if parasitization is delayed. The

effect of parasitization upon host egg production was strikingly apparent during September and October, when numerous *mexicanus* females showed a large proportion of unparasitized individuals with large egg masses in advanced stages of development. Parasitized females rarely contained eggs, and such eggs as were found were few and frequently discolored or collapsed.

TABLE III

COLLECTIONS OF ADULT GRASSHOPPERS TAKEN FROM AUGUST 24 TO OCTOBER 5, SHOWING RELATIONSHIP BETWEEN SUSCEPTIBILITY TO ATTACK AND SUSCEPTIBILITY TO PARASITIZATION BY *Neorhynchocephalus sackenii*

GRASSHOPPER SPECIES	NUMBER EXAMINED	PERCENT ATTACKED	PERCENT PARASITIZED
Arphia pseudonietana	65	2	0
Phoetaliotes nebrascensis	43	0	0
Camnula pellucida	423	35	0
Aeropedellus clavatus	18	40	0
Melanoplus bivittatus	32	50	30
Melanoplus gladstoni	15	40	40
Melanoplus mexicanus	1767	10	10
Melanoplus dawsoni	202	9	9

SUMMARY

Two nemestrinid flies encountered parasitizing grasshoppers in Montana were doing evident damage to the reproductive organs of their hosts. To determine the value of these insects as natural checks of grasshoppers, observations were made in 1951 of their behavior, life history, distinguishing characters, host preferences, and the effect of parasitization upon the hosts' reproductive capacity. This paper deals principally with *Neorhynchocephalus sackenii* (Will.), but for purposes of comparison includes data on *Trichopsidea clausa* (O.S.).

Neorhynchocephalus sackenii was observed parasitizing several species of grasshoppers in a large area near Bozeman, Montana, called the Cottonwood area. Flies began emerging in mid-July and laid large numbers of eggs in beetle holes on fence posts. Females were predominant. Flies were never observed mating or feeding. Newly hatched larvae were first observed on the posts on July 31. Some larvae were seen being blown from the posts by wind.

The presence of *sackenii* larvae in grasshoppers was first noted on July 31, when marks were seen in the host's abdomen where the parasites had penetrated. It was found that these penetration marks distinguished parasitization by this species from that by *clausa*, which left no such marks. This difference is probably due to the manner in which the two species gain entry to their hosts.

Grasshoppers were collected about every 10 days between July 31 and October 6 in order to follow the development of the parasite larvae. *Melanoplus mexicanus* (Sauss.), *M. dawsoni* (Scudd.), and *Camnula pellucida* (Scudd.) were the principal host species in the area. Grasshopper species differed greatly in susceptibility both to attack by the parasites and to effective parasitization. In *pellucida* and some other host species the parasites were unable to complete development, and attempted parasitization, though frequent, was ineffective. Populations of heavily parasitized species were very low, although the evidence was insufficient to show that this relationship was casual.

With but one season's work it is impossible to evaluate the effect of the parasitization upon the entire grasshopper population or upon the individual species. Observed parasitization in grasshopper collections ranged from zero to 62 percent.

Parasitization reduced the reproductive potential of the grasshoppers by destroying their ovaries and egg masses and by shortening their life span.

Mature *sackenii* larvae began to emerge from their hosts the first week in September, and emergence continued until the first heavy frosts in mid-October killed both hosts and the remaining immature larvae.

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TIME RELATIONSHIPS IN THE NEST CONSTRUCTION AND LIFE CYCLE OF THE ALKALI BEE[1]

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The alkali bee, *Nomia melanderi* Ckll., inhabits large nesting sites in inorganic sandy or clayey soils having abundant subsurface moisture. Alkaline flats or low mounds with scanty vegetation are usually chosen. There is one principal generation, which flies for about 6 weeks during July and August. Its progeny overwinter in their brood cells as naked prepupae.

A typical alkali bee nest consists of a vertical shaft from 6 to 8 inches deep leading from a spoil mound at the soil surface to a series of three or four branch burrows, which are 2 to 3 inches long and diverge from nearly a common level. The cells are oval chambers arranged in close series directly beneath the branch burrows and connected with them by entrance burrows from ½ to ¾ inch long. A well-developed nest often has one side burrow which is longer than the others and extends downward to a depth of 8 or 9 inches, where it branches to form another but smaller group of cells. The deeper series is contructed and provisioned after the main one. Otherwise there seems to be no relationship between location of cells and time of their construction. Cells may be built anywhere along a branch burrow, and several branches may be used in locating a consecutive series of cells.

A cell is first formed as a large wide-necked chamber at the bottom of the entrance burrow. It is then partially filled with fine soil particles to form a perfect oval closed in at the top to form a neck just wide enough to admit the bee. The walls are polished with a transparent, waxy material that is presumably applied with the glossa. The cell is then provided with a spheroid of pollen moistened with nectar. Finally, a large banana-shaped egg is attached at both ends to the top of the pollen ball, and a spiral ceiling is constructed over the cell. The finishing touch is a plug of earth in the entrance burrow.

In Cache Valley, Utah, during July 1952, we studied rates of nest construction and brood development by digging out a series of nests of known ages. This technique furnished data on the rates of cell preparation, food storage, oviposition, and larval development. It also helped us trace the development of several parasites.

Nests were marked with greenhouse stakes either in the late afternoon when they were started or early the next morning when the shape of the mound characterized a half-day-old nest (fig. 1). Marked nests were excavated for each day of age from 1 to 19. In addition, nests 12 and 36 hours and 22, 25, and 30 days old were excavated. Whenever possible, more than one nest of each age was examined. Some of the female adults captured during excavation were dissected to permit a count of the number of eggs remaining in the ovaries.

New females emerged in the mornings from 8 to 11. They left the site shortly and did not return until midafternoon. Males were abundant during both periods and made sure that no females were left unmated. After making brief visits to existing nests and several unsuccessful starts, most of the females were able to make a successful entry into the soil by about 4 p. m. on cool days and 6 p. m. on hot days.

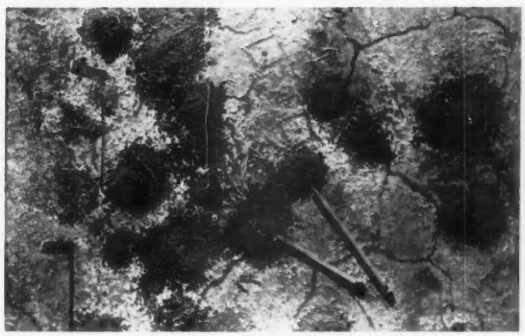

FIG. 1. Nest mounds: long pencil points to ½-day-old nest (flat top); short pencil to older nest (conical).

The bees were able to dig themselves under the moist clay surface in 7 to 12 minutes. Progress was then more rapid, the first inch of penetration taking 20 minutes and the second, 15 minutes. No additional record of the digging activity within the first 12 hours was obtained. However, the exposure of two nests a little more than 12 hours old and the size of mounds at others showed that the main burrow, usually 6 to 8 inches deep, was normally completed during the first night. The time required for digging the first 2 inches indicates that the burrow could be finished in 1½ to 2 hours. However, the burrowing probably proceeds more slowly as it becomes necessary to carry the material farther, and more time may be spent in perfecting the walls as the burrow is deepened. Digging activity during

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[2]In cooperation with the Utah Agricultural Experiment Station.

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the night could be determined by collecting and measuring the spoils material at regular intervals.

The bees spent most of the next day roughing in a series of brood cells and polishing one of them for the reception of food. Only rarely did we observe a bee bringing pollen to the nest during this first day of nesting activity. Generally the first cell was fully provisioned with a pollen ball on the second day; on the third day the first egg was laid, and the cell was walled off. This pattern of preparing a pollen ball on one day and laying an egg on it the next day was the rule for the next 20 to 22 days.

The irregularity of the total-cells line in figure 2 and its divergence from the theoretical line for a one-per-day rate reflect the bees' habit of roughing in several cells at once in advance of their needs. Our observations, which were made in the late afternoon, revealed many nests containing one polished cell empty of provisions. If all cell construction takes place at night, then two cells must commonly be made at a time, one being provisioned the next day. On the other hand, it is possible that, whenever a bee finishes provisioning a cell by early afternoon, it polishes a new one before evening. Only in the case of the 12-day-old nest was there more than one empty polished cell. This nest was examined after a 2-day rainy period and appears to represent an ability to take advantage of unusual circumstances.

TABLE I

CONTENTS OF CELLS OF 37 *Nomia melanderi* NESTS OF VARIOUS AGES. NEAR PETERSBORO, UTAH, JULY 1952

AGE OF NEST IN DAYS	NUMBER OF NESTS EXAMINED	NUMBER OF CELLS										TOTAL NUMBER OF CELLS
		ROUGH	POLISHED BUT EMPTY	PROVISIONED, NO EGG	POLLEN BALL + EGG	LARVA			FULL-GROWN LARVA	PREPUPA	PARASITIZED OR DISEASED	
						2-3 mm.	3-6 mm.	6-10 mm.				
1	4	2	1	0	0	0	0	0	0	0	0	3.0
2	4	3.7	0.5	0.5	0	0	0	0	0	0	0	4.7
3	3	4	0	1	0.7	0	0	0	0	0	0	5.7
4	2	5.5	0.5	1	1.5	0	0	0	0	0	0	8.5
5	2	4.5	0.5	0.5	2	0.5	0	0	0	0	0	8
6	1	6	1	1	2	1	0	0	0	0	0	11
7	2	5	0.5	1	1.5	1	1	0.5	0	0	0	10.5
8	2	4.5	0.5	0.5	2	1	1	1	0	0	0	10.5
9	2	5.5	0.5	0.5	2	1.5	2	1.5	0	0	0	13.5
10	2	6	0	1	2	1	2	1.5	0	0	0.5*	14
11	1	3	0	1	2	2	2	1	1	0	1*	13
12	2	4.5	3	1	1	1	2	1.5	2	0	0.5*	16.5
13	1	4	0	1	1	1	1	2	3	0	0	13
14	1	5	1	1	2	1	1	1	3	1	2*	18
15	1	2	0	1	2	1	1	2	2	3	0	14
16	1	1	0	2	2	1	2	2	3	3	1†	17
17	1	0	0	1	1	1	2	1	4	6	1‡	17
18	1	2	0	1	2	1	2	0	4	6	1†	19
19	1	3	0	1	1	2	3	2	3	4	1†	20
22	1	1	1	1	1	1	2	2	2	8	1†	20
25	1	1	0	1	1	0	1	2	3	6	2†	17
30	1	1	0	0	0	0	0	0	1	12	4§	18
TOTAL.....	37	74	10	19	29.7	18	25	21	31	49	15	291.9

*Larvae of sarcophagid flies.
†Puparia of sarcophagid flies.
‡Moldy *Nomia* larva (dead).
§Two cells with sarcophagid pupae and 2 with moldy *Nomia* larvae (dead).

The progress made in cell construction and brood development in 37 nests excavated at various ages up to 30 days is shown in table I. Figure 2, based on this table, illustrates how closely the bees adhered to a one-per-day rate in making their pollen balls and laying their eggs. The deceleration in these activities recorded for nests over 20 days old may have been caused by slower ovogenesis. Another probable contributing factor was parasitism of the adult bees by larvae of the conopid fly *Zodion obliquefasciatum* Macq. The developing maggots of this parasite progressively starve the ovaries and then crowd them out.

It is not known whether the oviposition rate is determined by the time required for provisioning cells or by the rate of ovogenesis. The latter is more logical, for one would expect more variation in the rate if external conditions, such as weather and availability of food, were the limiting factors. Furthermore, the drive to prepare cells at the usual rate even during inclement weather suggests a motivation from within.

During a typical day, then, a female alkali bee (1) lays an egg on a pollen ball and then seals the cell and plugs the entrance, (2) provisions the next cell with a pollen ball, and (3) polishes a new one. It is not known whether eggs are deposited in the evening after the day's activity or in the morning before the new flight period. Evidence based on accumulation of spoils material indicates that branch burrows and new cells are constructed at night.

with the usual size of a nest. Each ovary of the alkali bee is composed of 3 ovarioles. Four prenesting females that were dissected had 4 eggs in each ovariole (total 24), the anteriormost being quite small and translucent. A bee from a 12-day-old nest had 15 eggs, and additional eggs were not being produced. One from a 25-day-old nest had only 3 eggs remaining, one in each ovariole. All these dissections indicated a capacity of about 25 eggs. The largest nest

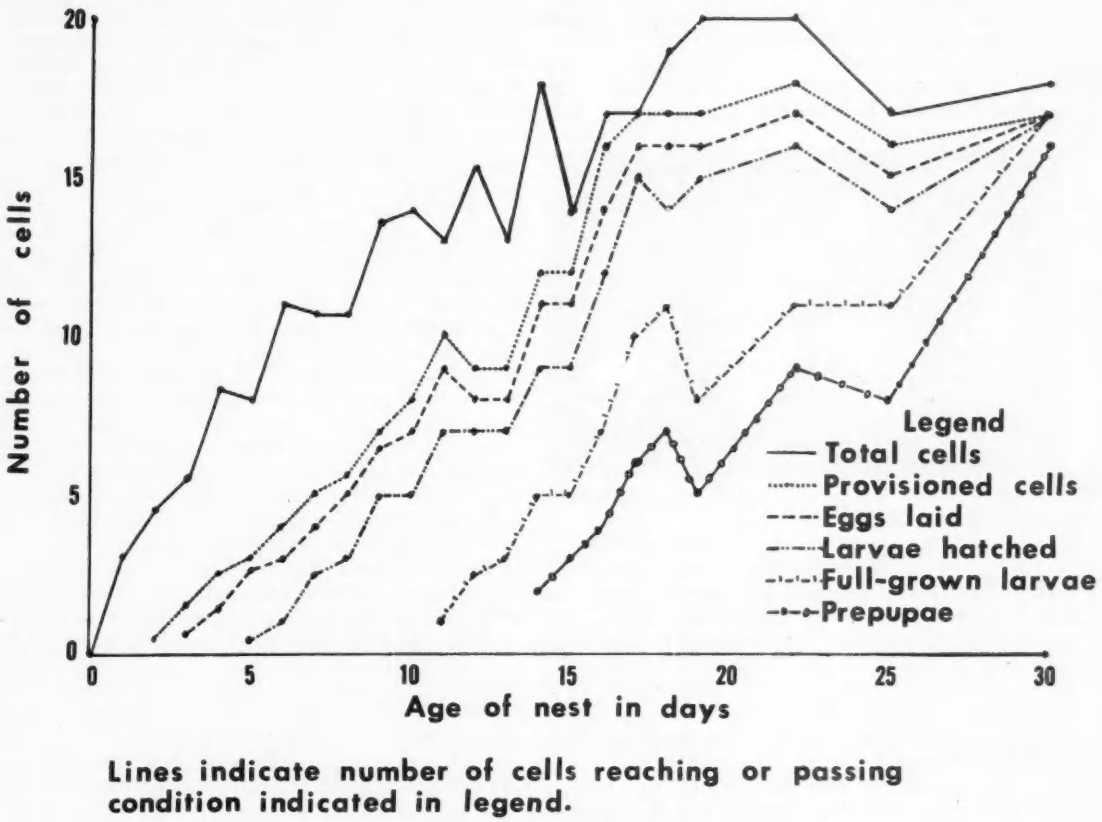

FIG. 2. Cell progress in 37 nests of *Nomia melanderi*. Petersboro, Utah, July, 1952.

According to our observations only one nest is prepared and provisioned by each female. A number of marked females were never seen again, but others, a few of which were observed for as long as 26 days, worked only in single nests. However, it is probable that a bee prevented from using a nest she had only begun to provision would start another. It would be of interest to know at what point in the progress of her nest building a bee would lose the instinct to start again.

Another line of evidence that the alkali bee does not ordinarily prepare more than one nest lies in a comparison of her egg-producing capacity

we found contained 24 cells with brood, and usually there were 15 to 20 cells with brood in a completed nest.

As indicated by the age of the nests in which eggs, developing larvae, full-grown larvae, and prepupae first appeared, the major developmental periods are as follows (table I): incubation, 2 days; larval growth, 6 days; transformation to prepupa, 3 days; total, 11 days. Most of these figures are corroborated by the numbers of each stage appearing in nests of various ages. For example, 2 full-grown larvae in 12-day-old nests, 3 in a 13-day-old nest, and 3 full-grown larvae plus 1 prepupa in a 14-day-old nest all point to a 6-day

period of larval growth if one assumes a one-per-day egg-laying rate. The relatively constant rate of larval development is evidenced by the one-per-day routine of nest development still discernible in the case of developing larvae and prepupae. This feature is readily seen in figure 2, where correction is made for the sarcophagid parasites which replaced *Nomia* in many of the cells.

There is no development of the prepupae until the late-spring sun warms the ground at the brood-cell level. The first change to be seen is an elongation of the thoracic region and a softening of the body wall (fig. 3). This stage, which lasts for a week or less, is sometimes called the propupal stage. Shedding of the prepupal skin

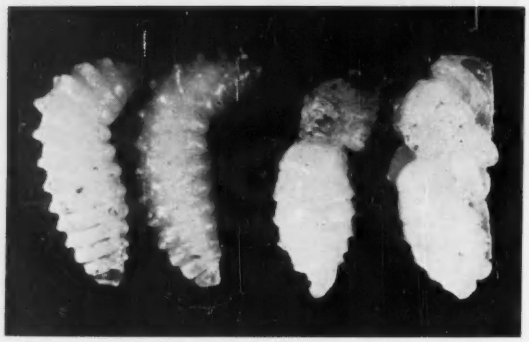

FIG. 3. Left to right: prepupa; "propupa;" pupa forming within "propupal" skin; pupa.

takes place in Utah in both June and July, depending upon temperature factors governed by soil type, cell depth, and surface vegetation. In the laboratory the pupal period generally lasts about 3 weeks. However, evidence from inspection of cells in the nesting sites indicates a lag of only about 2 weeks between the first appearance of pupae and the first appearance of adults in the cells.

Peak emergence of males precedes that of females by about 1 week, but there is considerable overlapping. The total period of emergence may last for nearly a month because of differences in temperature within the cells. The teneral adults spend their first 3 or 4 days hardening within their cells. Even after emerging from the ground, the adults have rather soft and glistening wings and must crawl about and take short "hops" for several minutes before making sustained flights. During this period the females are readily mated, as many males are already flying over the site.

Evidently there is a partial second generation in at least some localities of Utah. At sites in both northern and central Utah large numbers of freshly emerged males have been seen to appear suddenly in August at a time when males from the previous emergence were already old and tattered or gone altogether. More definite evidence of a second generation was found in August near Flowell, Utah, where a nesting site was discovered in some new soil used to plug a break in an irrigation pond. Nesting activity was nearly over, but several fresh-looking males were flying over the site. Digging revealed a number of white and pigmenting pupae of both sexes. Although this site was destroyed soon afterwards, it can be assumed that these pupae would soon have become the adults of a second generation, since the pupal stage of bees is always short. A logical method for learning more about the significance of this partial second generation would be to remove brood from an area within a nesting site in the spring before emergence. Then, if pupae can be found in this area the same year, the presence of second-generation bees on the site is established.

SUMMARY

On a nesting site of the alkali bee, *Nomia melanderi* Ckll., in western Cache Valley, Utah, 37 marked nests from 12 hours to 30 days old were excavated to chart the nesting activities of the female bee and the development of the immature stages to the prepupal condition.

Findings indicate that typically each female builds a single nest of 15 to 20 cells in about 30 days. A bee starts her nest late in the afternoon of the day she emerges from the soil, having first left the site to feed. Mating usually takes place on the site both before and during the nest-construction period. The main burrow is 6 to 8 inches deep and is completed the first night. The next day the first two or three cells are roughed in and one is polished. The following day this polished cell is provisioned with pollen, and on the third day an egg is laid on the pollen ball, after which the cell is closed. A daily routine of one egg laid, one cell provisioned, one cell polished, and one or more cells roughed in is thus established and maintained until 15 to 20 eggs have been laid. Thereafter the rate of these activities declines. The periods required for various phases of nest building and brood development are: prenesting and mating flight, ½ day; preoviposition period during which nest building progresses to the first finished cell, 2 days; incubation period, 2 days; larval growth, 6 days; transformation to prepupa, 2 to 3 days; egg to prepupa, 10 to 11 days.

The prepupal period lasts through the fall, winter, and spring, and pupation, which usually begins in June, requires 2 weeks. The teneral adult remains in its cell for 3 or 4 days before taking flight. Emergence of adults at a nesting site may last nearly a month with the peak for males preceding that for the females by about 1 week. Usually there is a single generation of adults in the summer, but evidence of a partial second generation has been found in some localities.

A MORPHOLOGICAL STUDY OF THE RESPIRATORY HORNS ASSOCIATED WITH THE PUPARIA OF SOME DIPTERA, ESPECIALLY OPHYRA ANESCENS (WIED.)[1]

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This study concerns the respiratory horns of three species of Diptera. "Respiratory horns" is the common name given to a pair of prong-like structures which occur on the dorsolateral aspect of the cephalic half of a number of pupae and puparia of Diptera, especially among Cyclorrhapha. De Meijere (1902) made the first systematic attempt to describe the structure of the respiratory horns in various families of Diptera, drawing information both from his own observation and from the scattered descriptions in the literature. Many interesting examples of respiratory horns in pupae have been described and figured in several papers dealing with the morphology of larvae and pupae of Diptera. The figures in these papers give a clear idea of the great variations in size, shape and structure of these horns, often described as prothoracic horns, trumpets, spiracles, siphons or gills. Their size varies from short, sessile and hardly perceptible to long and distinctly prominent projections in some pupae.

This study was restricted to the puparia of *Ophyra anescens* (Wied.), *Lucilia sericata* (Meig.) and *Musca domestica* Linn.; however much of the information was ascertained from *Ophyra anescens*. The species named are related in that they belong to the same large group (calyptrate Muscoidea), yet the larvae and puparia are distinctly different. The same is true for the respiratory horns that appear on the puparia of these species.

The purpose of this study was to determine the following facts regarding the respiratory horns; structure and development, time of appearance, size, location, the effects of temperature and humidity on their development, their function in respiration, and the relation between the size of horns and the respiration rate.

EXPERIMENTAL TECHNIQUES

The method used in the rearing of *Ophyra anescens* was a modification of the technique used by Dr. F. M. Snyder of the Chemical Corps Laboratory at Army Chemical Center, Maryland.

The larval medium consisted of whole milk (Klim), 200 gm.; Brewer's yeast (Fleischmann), 200 gm.; bacto-agar, 15 gm.; and tap water (boiling), 2 liters. The dried ingredients are added slowly to the boiling water and stirred continuously to insure thorough mixing. When the medium is cooled it is stored in sealed containers and kept in a refrigerator until needed. A simple modification of the Snyder technique was made by placing a small amount of sterilized sand on the surface of the medium three days after the larvae hatch. The author finds that this affords a better environment for the larvae to pupate and the puparia are much easier to collect.

The method used to rear *Musca domestica* was the standard technique specified by the Soap Blue Book (1953) for use in connection with the Peet-Grady test for household sprays.

The method used in the rearing of *Lucilia sericata* was essentially the same as the technique used by Frings (1941).

A small differential microrespirometer manufactured by the Micro-Chemical Specialities Company, Berkeley, California was used to measure the respiration rate in the various stages of pupal development.

To determine the function of the respiratory horns in pupal respiration, the following tests were made: (1) spiracular plugging, (2) dissections, and (3) dye penetration of the tracheal system.

Spiracular Plugging: In this test, three methods of plugging were used: (1) plugging the anterior and posterior spiracles before the respiratory horns had emerged on the puparia, (2) plugging the anterior and posterior spiracles after the respiratory horns had emerged, and (3) plugging the respiratory horns.

The material used for plugging was Duco household cement. Its toxicity to the developing pupa was tested previous to the experiment by placing a small drop of the cement on parts of the body other than the respiratory parts to be tested. It proved to be non-toxic for the adults emerged and without any noticeable effect.

Dissections: Two stages of the puparia were used primarily for dissection: those that had not developed the respiratory horns, and those that had well developed horns. Before dissections were made the puparia were placed on a small drop of Duco household cement and the cement was allowed to dry. The slide was then placed in a Petri dish containing 50% alcohol. Then with the aid of a microscope the dissections were made.

Dye Penetration: In this method of determining the function of the respiratory horns in respiration, a puparium with well developed horns was placed in a small Petri dish (1.2 x 2 cm.) and just enough water soluble dye (Methylene blue) was

[1]Based on dissertation submitted in partial fulfillment of the requirements for the degree Doctor of Philosophy in Entomology in the Graduate School of the Ohio State University. Date of acceptance, April 13, 1954.

poured over it to cover the tips of the horns. At the end of two minutes the puparium was removed from the dye and washed in tap water to remove any dye that remained on the external surface. Next the puparium was placed in a small drop of Duco household cement on a microscope slide and the cement was allowed to dry. After drying, it was placed under a microscope and dissected to show the tracheal system. The results of this method showed whether the dye was in the tracheal trunks leading from the respiratory horns or from those connected to the anterior and posterior spiracles.

In testing the effects of humidity on development of the respiratory horns, all readings were made with a bright, nickel-plated, dew-point bulb, similar to the one figured by Peterson (1953, plate 177: 2).

To obtain puparia of a known age, a method similar to the one used by Robertson (1936) was used. When a larva ceases to feed and begins to shorten in length, it is removed from the culture medium and transferred to a small Petri dish. When there is no further movement by the larvae, the time is checked and recorded on the Petri dish. The lack of movement and shortening of the body is interpreted as the beginning of the puparial stage. Thus, the age of the puparium is calculated in hours from the beginning of pupariation until the adults emerge.

DISCUSSION

There are many variations in the size, shape and detailed structure of the respiratory horns of dipterous pupae. They may be short, sessile and hardly perceptible as in *Musca domestica* (fig. 10), or they may be distinctly prominent and in some pupae (Psychodidae) reach a very great length (fig. 16). In the pupae of some *Ptychoptera* only one spiracle develops into a horn while the second spiracle is more or less atrophied.

Orthorrhaphous Pupae

Among the orthorrhaphous pupae (figs. 13, 15, 17, 19), the respiratory horns of *Psychoda alternata* Say will serve as a type.

Each horn (fig. 18) has the form of a curved tapering cylinder narrowed at the base, where an annulated region consisting of four or five thickened rings occur. Within the horn is a tube lined with chitinous felt, which De Meijere (1902) terms the "felt chamber", (F.C.). The felt chamber meets the wall of the horn at a number of thin circular regions. These regions De Meijere terms the pits (P), because of their likeness to similar structures in plant cells. The pits are irregularly arranged and communicate directly with the felt chamber.

The felt chamber communicates, through the annulated base of the horn, with a small tube shaped chamber which has a characteristic spiral shape thickening. This is termed the tracheal extension (T. E.).

The side of the tracheal extension is fused with the body wall, the line of fusion being marked by an elongate scar. At the lower end, the tracheal extension passes into the spiracular chamber (Sp.C.). The elongate scar of the tracheal extension terminates in a dark sclerotized plug, the closed pupal spiracle, which De Meijere terms the outer stigmatic scar (E.S.). It is connected to the spiracular chamber by a short chitinous thread, the scar strand (S.St.), which is the shrunken remnant of the tube through which the larval trachea were withdrawn. At the juncture of the scar strand with the spiracular chamber is a smaller inner stigmatic scar which connects the scar strand to the internal surface of the spiracular chamber.

From the spiracular chamber a trachea is given off that enters the prothoracic spiracle of the imago. This spiracle is the type found in most insects and consists of two semicircular sclerotized lips which can be closed by the con-

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EXPLANATION OF PLATE I

FIG. 1. Dorsal view of a 4-hour puparium showing the circular apertures (C.S.). *Ophyra anescens* (Wied.) X 20.

FIG. 2. Dorsal view of a 30-hour puparium showing respiratory horns. *O. anescens*. X 20.

FIG. 3. Lateral view of a 30-hour pupa dissected from puparium. *O. anescens*. X 27.

FIG. 4. Lateral view of the respiratory horn. *O. anescens*. X 120.

FIG. 5. Dorsal view of a 4-hour puparium of *Lucilia sericata* (Meig.). X 18.

FIG. 6. Dorsal view of a 30-hour puparium with respiratory horns. *L. sericata*. X 18.

FIG. 7. Ventral view of a 30-hour pupa dissected from puparium. *L. sericata*. X 20.

FIG. 8. Lateral view of the respiratory horn. *L. sericata*. X 140.

Fig. 9. Dorsal view of a 4-hour puparium of *Musca domestica* Linn. X 20.

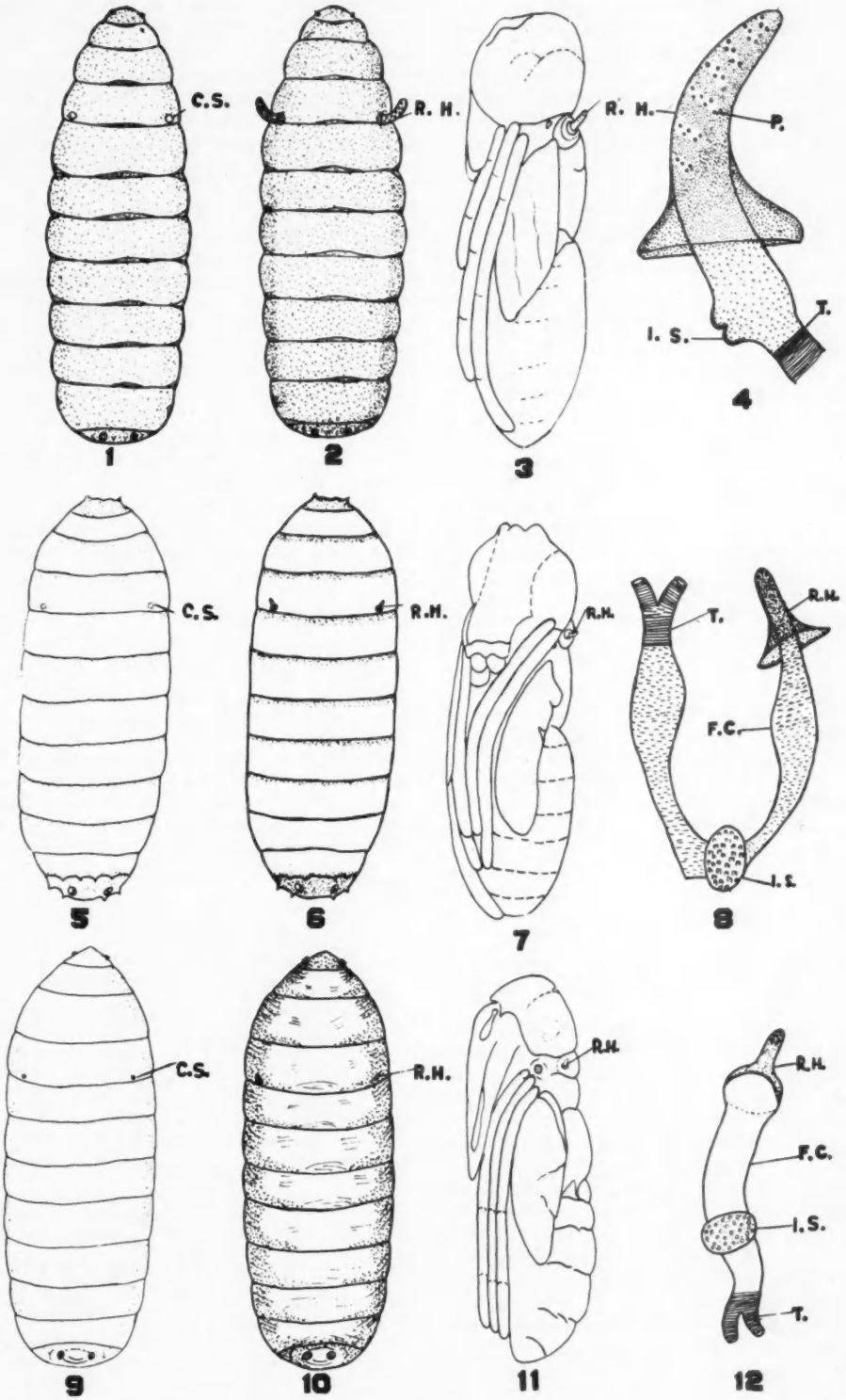
FIG. 10. Dorsal view of a 30-hour puparium of *M. domestica*. X 20.

FIG. 11. Lateral view of a 30-hour pupa dissected from puparium. *M. domestica*. X 22.

FIG. 12. Lateral view of respiratory horn of *M. domestica*. X 160.

ABBREVIATIONS USED IN THE FIGURES

A.C. Anterior Chamber
A.R. Annulated Ring
A.T. Anterior Tracheal Tube
B. Ph. Buccopharyngeal Armature
C.S. Circular Spots
E.S. External Stigmatic Scar
F.C. Felt Chamber
I.S. Internal Spiracle
L. Closing Lever
MEM. Membrane
P. Pits
R.H. Respiratory Horns
SP.C. Spiracular Chamber
S.ST. Scar Strand
T. Trachea
T.E. Tracheal Extension


C.S.
1
R. H.
2
R. H.
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P.
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traction of a band of muscles running between them. This constitutes the closing mechanism of the imago trachea. At the upper end of the tracheal extension is a heavily chitinized lever (L.) which constitutes the closing mechanism of the pupal trachea. This closing mechanism is narrowed basally, but broadens apically and bifurcates into two short arms which partially encircle the tracheal extension. At the tip of the lever is a closing muscle which by contraction and expansion opens and closes the trachea.

Cyclorrhaphous Pupae

The pupal stage of the cyclorrhaphous Diptera is always enclosed within the cuticle of the last larval instar. After it shortens, it becomes a distinctly brown case which is called a puparium. Often the space between the pupa and the puparium, especially in the anterior region, is filled with air. In the majority of the acalyptrates the pupae have a pair of prothoracic spiracles which are enclosed within the puparium and are known as internal spiracles. Each spiracle is composed of a more or less protruding felt chamber covered with numerous spiracular papillae. In the great majority of the calyptrates the felt chamber of the prothoracic spiracle of the pupa, in addition to the internal spiracle develops into a more or less sclerotized horn covered with spiracular papillae (figs. 4, 8, 12, I.S. and R.H.). These protrude through small circular apertures in the wall of the puparium (C.S.).

The detailed development of the respiratory horns was studied only in the pupae of *Ophyra anescens*. One of the most fascinating phenomena observed in this study was the protrusion of the horns through the hardened cuticle of the puparium. Protrusion is possible because of the presence in the wall of the puparium of two small circular clear spots (fig. 1, C.S.) where the cuticle is thin and fragile. These spots are light brown in color and surrounded by a brown ring. They first appear in 3 to 4-hour puparia and persist throughout the prepupal or puparial stage.

Dissection of a 10-hour puparium shows that the respiratory horns are developed and lie parallel to the length of the body (fig. 24) whereas, after protrusion, they are more nearly perpendicular to the body.

About 18 hours after pupariation the anterior end of the pupa contracts leaving a free space. On each side of the pupa the partially evaginated respiratory horns (R.H.), which, according to Keilin (1944), emerge from apertures of their imaginal disks. These horns are light brown in color and show distinctly small spiracular papillae. Approximately 25 hours after pupariation the horns assume their final shape and structure. Three or four hours later the pupa contracts drawing the respiratory horns posteriorly, away from the anterior end, until their tips appear just beneath the two circular spots. During this period the pupa breaks away from the anterior tracheal tubes of the larva (fig. 26). The pupa then makes a few forward and backward movements, pushing the tips of the horns against the thin chitinous membranes of the circular spots until the membranes are broken. Further movements of the pupa push the horns through the broken membranes. Soon they are completely outside the puparium where they are readily visible to the naked eye. The whole process is completed within 1 or 2 minutes.

According to Keilin (1944) the contraction of the pupa is due mainly to the evagination of the imaginal disks of the head. It is remarkable to note that the length of the respiratory horns and the predetermined clear spots on the first abdominal segment of the puparium are so adjusted that the tips of the horns having moved backward about 2 mm. are brought directly against the two fragile spots, through which they will emerge. In spite of this delicate adjustment, the extrusion of the respiratory horns is almost always successful. However, there are times when one or both horns fail to perforate the fragile spots and slip forward remaining within the puparium. If one horn is extruded the pupa may develop normally, but if both fail to emerge, the pupa does not develop into an adult fly. This may be due to the lack of oxygen which results in the death of the pupa.

Time of Emergence

The time of emergence of the respiratory horns on the exterior of the puparium is variable in the three species studied. In *Musca domestica* reared at a temperature of 80° F. and a relative humidity around 50%, they appear externally 18–20 hours after pupariation and are visible in

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EXPLANATION OF PLATE II

FIG. 13. Culicidae, *Aedes aegypti* (L.). A lateral view of a yellow fever mosquito pupa showing the respiratory horn. X 30.

FIG. 14. Enlarged view of the respiratory horn of *A. aegypti* pupa. X 82.

FIG. 15. Ventral view of a cranefly pupa showing respiratory horns. Tipulidae, *Tipula* sp. X 8.

FIG. 16. Enlarged view of the respiratory horn of *Tipula* sp. X 26.

FIG. 17. Ventral view of Psychoda pupa. *Psychoda alternata* Say. (Psychodidae) X 8.

FIG. 18. Enlarged view of respiratory horn of *P. alternata*. X 29.

FIG. 19. Dorsal view of a salt marsh fly pupa, Ephydridae, *Brachydeutera argenata* (Walker). X 15.

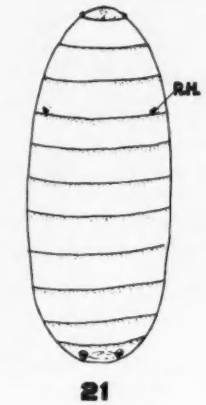
FIG. 20. Enlarged view of the respiratory horn of *B. argenata*. X 60.

FIG. 21. Dorsal view of the puparium of *Phorocera claripennis* (Tachinidae). X 18.

FIG. 22. Enlarged view of the respiratory horn of *C. claripennis* X 175.

FIG. 23. Lateral view of the puparium of *Meredon equestris* (F.). (Syrphidae). X 9.

FIG. 24. Enlarged view of the respiratory horn of *M. equestris*. X 55.



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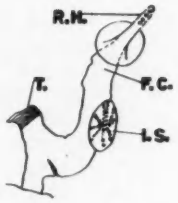

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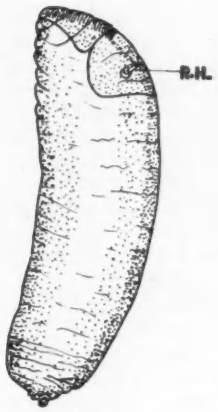

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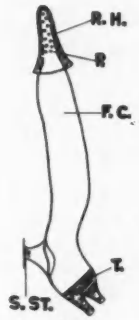

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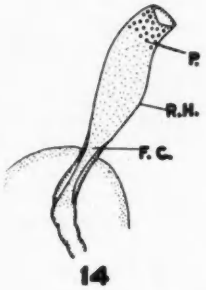

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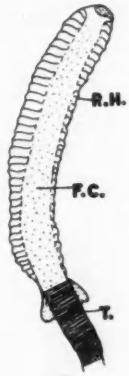

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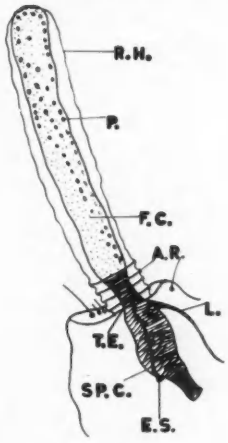

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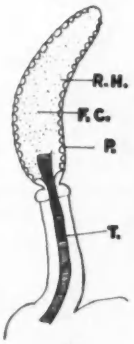

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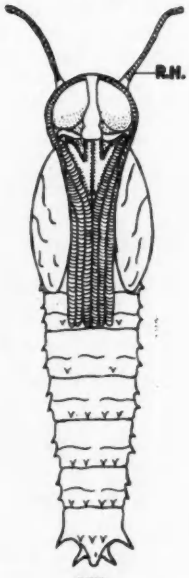

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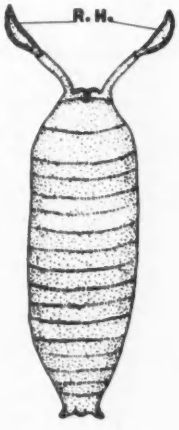

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profile as tiny nodules (fig. 10). In *Lucilia sericata*, the appearance of the horns is quite variable even under optimum rearing conditions (temperature 78° F., humidity 40%). In some of the puparia they begin to emerge 20–25 hours, and in others from 30–50 hours after pupariation. In unusual cases the horns emerge just a few hours before emergence of the adults.

The emergence of the respiratory horns is not so variable in *Ophyra anescens*. On the average, they began to emerge between 28–30 hours after pupariation. No further emergence of these horns were observed beyond 30 hours after pupariation. Isolated 30 to 50-hour-old puparia devoid of horns do not develop further. Dissections revealed that the pupae within were dead.

It is evident that in the three species studied, the horns do not emerge for sometime after pupariation, but their site can always be determined by a pair of pale circular spots on the laterodorsal surface of the puparia (figs. 1, 5 and 9 C.S.). These are visible immediately after the puparia are formed.

Location

The location of the respiratory horns on the puparium is approximately the same for each species studied. They appear in the conjunctiva between the fifth and sixth visible segments halfway between the meson and the lateral margin on the dorsal aspect. Several investigators have reported that these structures are located between the fourth and fifth segments; however, this may be due to the fact that only 11 segments are recognizable on the puparium because the pseudocephalon of the larvae is completely withdrawn. Actually there are 12 segments in each puparium.

Size

The size of the horns affords a good basis of comparison among these species. They are largest in *Ophyra anescens* and can be seen with the naked eye (fig. 2). They are from 0.5–1.0 mm. in length and approximately 0.25 mm. in width, with blunt ends and directly anteriorly. They are much smaller in *Lucilia sericata* and cannot be seen readily without the aid of a microscope (fig. 6). They range in size from 0.188–0.25 mm. in length and approximately 0.141 mm. in width. They are widest at the base and taper anteriorly. In *Musca domestica* they resemble those found in *L. sericata*, but are decidedly smaller and can only be seen with the aid of a microscope. They are approximately 0.188 mm. in length and 0.105 mm. in width.

Effects of Temperature and Humidity

During this investigation it was noted in several instances that the appearance of the respiratory horns on the puparia was often delayed. Occasionally they did not emerge during the entire course of pupal development. The reasons for this situation were investigated. After checking the conditions under which the flies were being reared, it was thought that the failure of emergence of these horns might be due to a decrease in relative humidity within the culture jars at the time pupation, for it was noted that the relative humidity inside the jars during this period was less than 45%. Measures were taken to increase the humidity in the jars, especially among the puparia of *Ophyra anescens*.

To increase the humidity in the culture jars, a supersaturated solution of calcium hydroxide was poured into a small beaker and placed on the top of the paper towels inside the culture jars. The jars were then covered with a piece of muslin cloth and placed in a constant temperature cabinet with a temperature of 82° F. Later examinations showed that the relative humidity had increased to 58% and the horns had developed on most of the puparia. At this point it was assumed that the delay or failure of the horns to appear was due to a decrease in relative humidity in the culture jars at the time of pupation. To test the validity of this assumption, other cultures with high relative humidity were set up under the same conditions except that they were placed in the temperature cabinets where the failure of the respiratory horns to develop was first noticed. In these cabinets it was noted that the temperature fluctuated between 75° and 89° F. The results from these cultures were the same as in previous cultures, namely, no horns emerged on the puparia.

At this point it was decided to test the effects of both temperature and humidity on the development of the respiratory horns. This was done by placing a culture jar of first instar larvae containing the super saturated salt solution and one without a salt solution in constant temperature cabinets (82° F.) The results from

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EXPLANATION OF PLATE III

Ophyra anescens (Wied.) Anthomyidae

FIG. 25. Dorsal view of a 10-hour pupa within the puparium. Note position of the respiratory horns. X 20.

FIG. 26. Enlarged view of the anterior portion of a 10-hour pupa. X 45.

FIG. 27. Dorsal view of a 28-hour pupa immediately before emergence of the respiratory horns. Note position of horns. X 20.

FIG. 28. Dorsal view of a 30-hour pupa showing the respiratory horns immediately after emergence from puparium. X 20.

FIG. 29. Enlarged view of Fig. 27. X 45.

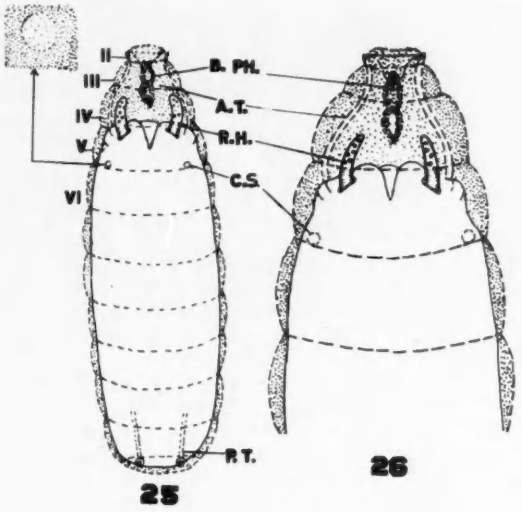
FIG. 30. Enlarged view of Fig. 28. X 45.

FIG. 31. Enlarged ventral view of Fig. 28. X 45.

FIG. 32. Enlarged view of the anterior ventral portion of a 90-hour pupa. X 45.

FIG. 33. Dorsal view of a puparium immediately after emergence of adult. Note horns attached to the wall of puparium. X 20.

FIG. 34. Enlarged ventral view of a puparium after emergence of the adult fly. X 45.



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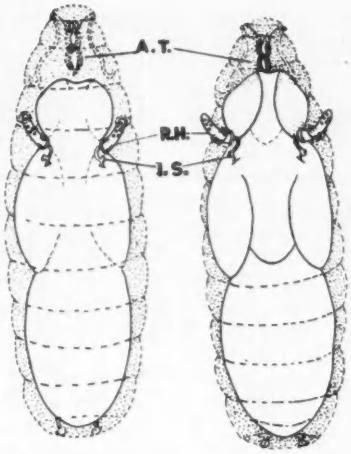

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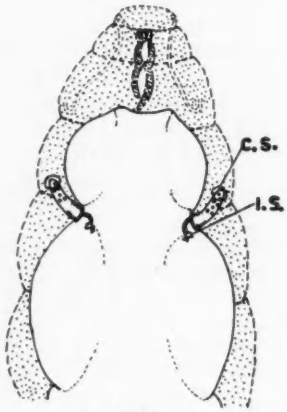

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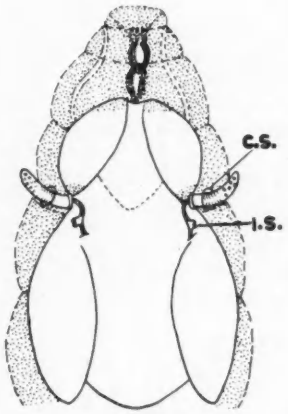

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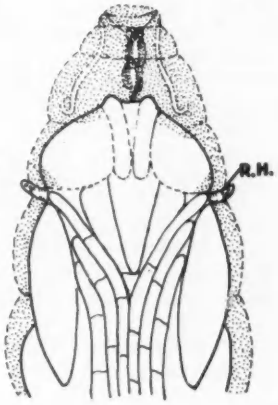

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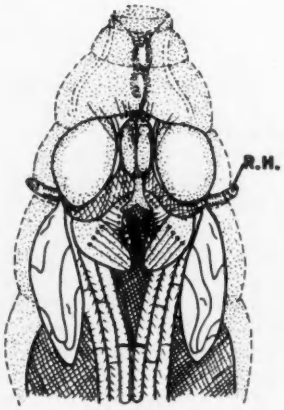

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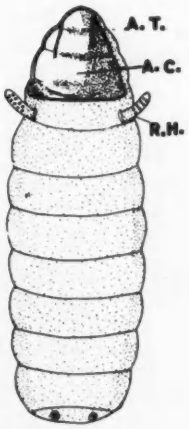

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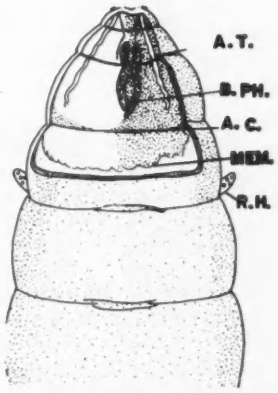

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this test revealed that the puparia in both culture jars developed respiratory horns at approximately the same time.

Thus from this experiment the results indicate that a fluctuating temperature rather than a decrease in relative humidity influenced the development of the respiratory horns on the puparia.

Functions of the Respiratory Horns

It has long been suspected that the respiratory horns are the sole means of pupal respiration in those forms that possess them. To determine the functions of these horns in respiration the following tests were made: (1) spiracular plugging, (2) dissections, and (3) dye penetration of the tracheal system.

Spiracular plugging: The result of this test showed that in young puparia, that is, those devoid of horns, the tracheal system of the last stage larva still functions. The anterior and posterior spiracles of 16 three-hour-old puparia were plugged with Duco household cement and of this number only one adult emerged. In older puparia, those with horns developed, the anterior and posterior spiracles of the last stage larvae no longer functions. Of the 16 (44-hour-old) puparia tested, 15 adults emerged. However, when the respiratory horns are plugged with cement, the flies will not emerge. Of the 16 puparia tested in this fashion only one adult emerged.

Dissection: If a 3-hour old puparium is dissected, the tracheal tubes of the last stage larva are seen connected to the developing imago and are seen pressed against the inner surface of the puparium (fig. 27).

Dye Penetration: The results of this test showed that if young puparia, devoid of respiratory horns, are placed in the dye, the dye will penetrate the entire length of the developing imago. However, in puparia, those with horns, the dye is only seen in the tracheal tubes leading from the respiratory horns.

Thus from these tests the results indicate that the respiratory horns are the sole means of pupal respiration.

RELATIVE RATE OF RESPIRATION IN PUPAE

After the various experiments had been performed to determine the function of the respiratory horns, it was decided to test the effect of size and structure of the horns on the respiration rate in several stages of pupal development. It was suspected that the difference in the size and structure of these horns in the three species studied, *Ophyra anescens*, *Lucilia sericata*, and *Musca domestica*, was due to the difference in the rate of respiration. As a means of testing this hypothesis, a Misco type microrespirometer similar to the one used by Barth and Kirk (1942) was used as a device for measuring the respiration rate.

Six stages of pupal development in the three species of flies were tested with this apparatus. They were the last stage larvae, prepuparia (when the larvae begin to shorten in length), 3-hour puparia, 28-hour puparia, 46-hour puparia, and 75-hour puparia. Four replicates of each stage were tested.

The results of this test revealed that respiration was highest in the stages of *Lucilia sericata* and lowest in the stages of *Ophyra anescens*. There is a marked decrease in the respiratory rate in passing from the larval stage to the pupal stage reflecting the decrease in metabolic rate which is the general rule for all holometabolic insects during this period.

It is evident that the difference in the size and structure of the respiratory horns in the three species does not influence the respiration rate. If the hypothesis were true, the rate of respiration would be greater in *Ophyra anescens* than in the other two species, since the respiratory horns are much larger and all three species about the same weight.

SUMMARY

1. The pupae of cyclorrhaphous Diptera are always enclosed within the last larval skin, the puparium. The prepupal stage is defined as that stage when the larva ceases to feed, becomes quiescent, and the prothoracic spiracles of the larva project cephalad. The term pupariation is used to describe this process.

2. As a representative of orthorrhaphous pupae, the respiratory horns of the pupa of *Phychoda alternata* (Say) are described. Within each tubular horn lies the felt chamber, which meets the horn wall at a number of circular regions, the pits, and communicates, through the annulated base of the horn, with the tracheal extension. This is continuous, at the lower end, with the spiracular chamber, from which a trachea leads to the prothoracic spiracle of the developing imago. At the upper end of the tracheal extension lies the closing mechanism consisting of a highly chitinized lever attached to a band of muscle. Another closing mechanism is found in the prothoracic spiracle of the developing imago.

3. In the pupae of cyclorraphous Diptera there is a pair of prothoracic spiracles enclosed within the puparium and are known as internal spiracles. Each prothoracic spiracle is composed of a more or less protruding felt chamber of the prothoracic spiracle is drawn out into a well developed sclerotized horn covered with spiracular papillae. In the majority of the calyptrates the felt chamber of the prothoracic spiracle is drawn out into a well developed sclerotized horn covered with spiracular papillae and protrude through a small circular aperture in the wall of the puparium.

4. An account is given of the development of the respiratory horns of *Ophyra anescens*

(Wied.). The horn apparently arises as an outgrowth from the prothoracic imaginal disk of the developing imago. Fully developed horns at first lie parallel to the length of the body, whereas, after protrusion they are perpendicular to the body. About 18 hours after pupariation the pupa contracts, which is apparently due to evagination of the imaginal disks in the head. This contraction of the pupa brings the tips of the horns backward so that they lie directly beneath the two fragile spots in the wall of the puparium. The horns are completely developed and extruding from the puparium 28–30 hours after pupariation.

5. The results from the study of the respiratory horns found in the pupae of *Ophyra anescens* (Wied.), *Musca domestica* Linn.and *Lucilia sericata* (Meig.), may be summarized as follows: (1) the time of emergence of the respiratory horns is somewhat constant in the puparia of *O. anescens* and *M. domestica*, but quite variable in *L. sericata*, (2) the location of the horns is the same for each species, namely the conjuctiva between the fifth and sixth visible segments, on the dorsal side, (3) there is considerable difference in the size of the horns, being largest in *O. anescens*, intermediate in *L. sericata* and smallest in *M. domestica*, (4) the results obtained from spiracular plugging of the tracheal system, dissections, and dye penetration of the tracheal system indicate that the respiratory horns are the sole means of pupal respiration, (5) the size and structure of the respiratory horns has no influence on the respiration rate in the developing imago, for results show that although the respiratory horns found in the puparia of *O. anescens* are much larger than those found in the other two species, the respiration rate is less, and (6) it appears that fluctuating temperature rather than humidity affects the development of the respiratory horns, especially in *O. anescens*.

6. The structure of the respiratory horns found in cyclorrhaphous pupae differ from those found in orthorrhaphous pupae in that, (1) the felt chamber of cyclorrhaphous pupae is an extension of the prothoracic spiracle and is connected directly to the spiracle, (2) there is no tracheal extension leading to the spiracular chamber, (3) there is no closing mechanism in the trachea, and (4) the respiratory horns in general are much smaller and located on the first abdominal segment of the puparium.

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NOTES ON THE FEEDING PREFERENCES OF HABROBRACON ADULTS (MICROBRACON HEBETOR (SAY); HYMENOPTERA, BRACONIDAE)

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Honey adulterants. In the course of investigations on the genetic and developmental effects of ingested radioactive materials (A.E.C. Contract No. AT–(40–1)–1314), unexpected difficulty was encountered when female *Habrobracon* refused to feed on honey to which calcium chloride had been added. Previously females from the same inbred laboratory stock had fed freely on honey considerably adulterated with the phosphates and sulfates of cations other than calcium. Unfortunately many of the radioactive isotopes prepared by the Oak Ridge National Laboratory are available as catalog items only in chloride form and in HCl solutions.

In order to determine the palatability for *Habrobracon* a survey was made of possible honey adulterants useful in ingestion experiments. A series of molar solutions was employed. Mixtures of these solutions in known proportions were presented in droplet form to individual braconids in separate shell vials (20 by 65 mm). Samples of about five wasps were tested with each mixture on a number of days until a total of 345 wasps had been considered. The wasps used were starved until their abdomens were obviously flattened. Taken as evidence of feeding was the swollen abdomen in the crop region.

[1]A contribution from the Genetics Faculty, North Carolina Agricultural Station, Raleigh, North Carolina. Published with the approval of the Director of Research as Paper No. 555 of the Journal Series. Accepted for publication April 13, 1954.

Results of 50/50 honey mixtures in order of preference were as follows:

Nitrate Sodium	12.50%
Nitrate Calcium	13.34
Chloride Strontium	27.27
Iodide Sodium	37.50
Bromide Sodium	80.00
Acetate Calcium	84.21
Bromide Calcium	93.34
Acetate Sodium	100.00
Sulfate Sodium	100.00

In additional experiments using mixtures of 66 parts of solution to 33 parts of honey, and 75 parts of solution to 25 parts of honey, preference remained in the same order with acetate and sulfate successfully fed to 100% of the wasps. Feeding at mixtures of other compounds fell off to the lowest results with nitrates. No wasps fed on nitrates when proportions were 75/25.

Subsequently we have tested molar sodium citrate in several mixtures using 493 wasps. At the 66/33 level we find 50% of the wasps feeding. In setting up experiments with strontium 89 as the citrate we have succeeded with feeding 91% of starved wasps with 50/50 mixtures based on solutions of less than 1 molar.

It should be emphasized that taste rather than any other sense appears to be involved in this matter. Of the hundreds of wasps we have observed it was a very unusual individual which did not walk up to the droplet of adulterated honey shortly after it was introduced into the vial. Only after lowering the mouthparts into the droplet did a wasp lose interest, if it were a case of refusal. Furthermore, in a number of feeding failures, wasps which never fed returned repeatedly to investigate the droplet. Presumably the odor of honey could be serving as the attrahent here while the taste of the mixture is disappointing.

To our knowledge only one similar investigation has been performed with winged Hymenoptera. This was with honey bees where von Frisch (1934) discovered an aversion to saccharose solutions adulterated with NaCl while quite bitter mixtures of such things as quinine were freely ingested. Incidentally the sensitivity to salt was found to be even greater with bees than with humans.

Caterpillar interest in the male. Traditionally, adult males have been considered to be entirely indifferent to host caterpillars (Whiting 1932, Martin 1947) and it has been maintained that their source of food is limited to a single type-group comprising rich sirups and sirupy fruits (Grosch 1950). A recent series of observations during experiments with dyed host caterpillars (*Ephestia*) indicates that this suggested principle is not a hard and fast rule.

Paralyzed pre-stung *Ephestia* larvae had been injected with saturated aqueous solution of neutral red and presented to groups of wasps made up of both sexes. The purpose was to obtain wholesale quantities of fertilized eggs on the colored caterpillars. An interesting aspect of studies with this vital dye is its accumulation in the urate cells and its excretion by way of the silk (Grosch 1952). Three days after adults had been placed in closed petri dishes with red hosts we were greatly surprised to detect pink tinted abdomens on several males. Upon close examination 36% of the males were found to have neutral red deposited in the abdominal urate cells. Upon dissection several of such males were found with heavy masses of stained material in the lumen of the digestive tract.

The only possible source of neutral red was the host caterpillar. This was the initial phase of the first experiment with vital dye within six months (*Habrobracon* have a 10 day generation and about a 30 day life span at 30° C, the routine temperature used). Injected caterpillars had been carefully blotted on absorbent paper before transfer to the clean glassware used as containers. The conclusion that some males will feed from caterpillars in inescapable. However, the males which had so fed did not look well-fed and there seems to be no point in attempting to employ caterpillars in attempted routine feedings of males. No male has yet been observed while feeding on a caterpillar so it is not known if the needle puncture is used or some other break in the epidermis.

We are aware of the possibility that a dye may have some power of attraction and that males may not visit non-dyed caterpillars under normal conditions. However the answer is not easily forthcoming because males show no preference between distilled water and aqueous neutral red. All males, in samples of 50 each, found droplets of either type with facility when enclosed therewith in standard laboratory glassware.

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NOTES ON THE FAMILY LEPTINIDAE INCLUDING A NEW RECORD OF LEPTINILLUS VALIDUS (HORN) IN NORTH AMERICA (COLEOPTERA)[1]

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Following a recent investigation conducted to determine the incidence of tularemia in northern Minnesota beavers, a small number of adult beetles taken from the fur of these animals were sent to the senior author by Mr. Milton Stenlund, of the Minnesota State Department of Conservation, who stated that the beetles frequently had been observed on beavers during the course of the investigation and requested information concerning the economic importance of the beetle.

Examination revealed that these were not the beetle, *Platypsyllus castoris* Ritsema, commonly found on beavers, but belonged to the family Leptinidae, a group commonly referred to as "mammal-nest beetles." The junior author subsequently found them to be *Leptinillus validus* (Horn), a species described from the Hudson Bay area by George H. Horn in 1872.

The University of Minnesota insect collection was found to contain no Minnesota records for this species. There were, however, three specimens which were originally a part of the Otto Lugger collection. Unfortunately they bear little data and all specimens lack dates of capture. One specimen is without locality data, one has an Alaska locality label and the third has a label bearing the abbreviation "W.T."

A review of the literature on this species reveals that specimens have been reported only from the Hudson Bay area (Horn, 1872), Alaska (Riley, 1889) and the Chapleau Forestry District of Ontario (Judd, 1954). In an attempt to obtain distribution records which would reveal whether the species had been taken previously in the United States, letters were sent to a number of universities and other likely depositories in both the United States and Canada. Of the twenty-nine institutions contacted, only seven possessed specimens of *Leptinillus validus*.

According to James A. G. Rehn (*in litt.*) the type of the species is housed in the collection of the Academy of Natural Sciences of Philadelphia. It bears the label H(udson) B(ay) T(erritory). The Academy collection contains five other specimens which are labeled solely R(ussian) A(merica) (Alaska?).

Correspondance from Robert E. Olson states that the collection of the University of Maine at Orono contains a number of larvae and adults, both having been obtained from the fur of Maine beavers. These were obtained from beavers freshly removed from traps in icy water at Sebeois, Penobscot County, Maine, and at Sebec, Piscataquis County, Maine (January 7, 1947). Adults only were obtained from beavers at Glenwood, Aroostook County, Maine (February 1938). A number of adults from the latter locality were sent to the United States National Museum and to the Illinois Natural History Survey Division at Urbana, Illinois.

The Department of Agriculture collection at Ottawa, Canada, contains four adults and several larvae taken from beavers at Lampriere (about 52° 26′ N., 119° 19′ W.), British Columbia (no date stated); Fawn River (South of Fort Severn, about 55° N., 88° W.), Ontario, May 1953 and Black River (46° 20′ N., 77° 30′ W.), Pontiac County, Quebec (no date stated) (W. J. Brown, *in litt.*).

The Michigan State College collection contains a single specimen, formerly of the McMillan collection, which bears the following abbreviations upon the label on the pin: "Q—Roug., Queb., Provan." (Quebec ?) (Herman King, *in litt.*).

According to G. J. Spencer (*in litt.*), the collection of the University of British Columbia contains twenty-five adult specimens obtained from beavers at Bowrun Lake, British Columbia, September 10, 1948. He also states that a single specimen was obtained from a beaver lodge, unoccupied, in Caribou County, British Columbia, June 1949.

W. W. Judd (1954) records eight larvae taken from *Castor canadensis* Kuhl in the Chapleau Forestry District V, Crichton, Ontario, January 21, 1954.

The Minnesota specimens, a new state record, were obtained from living and dead beavers trapped at Snowbank Lake and Maniwaki Creek, both in Lake County, September 1952.

In the absence of any published biological studies on this species the information obtained through correspondence and our own observations would appear to suggest several points of interest concerning the biology of *Leptinillus validus*.

The relationship between the beetle and its beaver host appears to be well established, the beetle existing as an ectoparasite of the beaver.

The larvae have been recovered exclusively from the fur of the host and only during the winter months. This would suggest that the species is single brooded, the larval stages occurring during the season when the beaver is least active. In the future, careful examination

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of the nesting debris should be made in situations where beavers have been found infested. Such has not been done, to our knowledge.

The literature concerning the habits of this family pertain almost exclusively to *Leptinus testaceus* Müller, which, according to collection records, is the most common member of the family.

This species was described from individuals which were taken from a field mouse (species ?). In the description of this beetle the author concluded that it was an ectoparasite (Müller, 1817).

In a one-page note concerning this species, Fauvel (1863) expressed the belief that reports concerning the ectoparasitic habits of *L. testaceus* were erroneous. He believed that the beetles were not so much concerned with the rodents as they were with the fungi which "invariably are found to line the burrows of the nests of the rodents." Hamilton (1891) was of a similar opinion in that he believed collection records did not support the suggestion that the beetles were parasitic. American capture records to that date indicated that the beetles had been taken only once from a host. It was his opinion that inasmuch as the beetle has been found frequently independent of host animals, the proper term to apply to it in its relation to rodents would be "frequently inquilinous."

The later reports of a number of European investigators record this species from the nests of wild bees (Eichhoff, 1866; Gorham, 1869; Lesne, 1896; Rye, 1866). It was the general opinion of these authors that the beetles were inquilines, feeding on honey and pollen, and that they were transported from nest to nest by rodents and insectivores raiding the nests in search of food. Consequently the relationship with the mammal host was thought to be that of phoresy.

In 1922, Jeannel presented a comparative study of *Leptinus* and *Platypsyllus* with the purpose of demonstrating the close relationship existing between the two species. He reviews the knowledge of the habits of *Leptinus* and concludes that it is a "xenophile" (host-loving) showing many adaptations which would suggest parasitic existence.

> After having studied its morphology in detail and especially the remarkable specialization of the head and mouth parts, it is difficult not to look upon it (*Leptinus*) except as a true ectoparasite—temporary ectoparasite to be sure, as it is a known fact that it leaves its host during a large part of its existence. (Free translation from the French text, Jeannel, 1922, page 562.)

The characters discussed by Jeannel which indicate adaptation to parasitic life by *Leptinus* and *Platypsyllus* are: (1) flattening of the body, (2) depigmentation, (3) loss of organs of visual reception, (4) loss of membraneous wings, (5) immobilization of the head and specialization of the mouth parts (an adaptation to feeding on stationary food, *i. e.* sebaceous exudates and dermal scales), (6) fusion of the sternal sclerites and loss of the sutures, and (7) the formation of tenent spines (less pronounced in *Leptinus*).

The only characteristics of *Leptinus* which Jeannel feels may be interpreted as an indication of adaptation to subterranean existence of the type described by Fauvel are the long antennae, which are thought to compensate for the loss of visual organs, and the remarkable agility of the insect.

The most extensive study of the biology of this species was done by Rüschkamp. Since larger numbers of adult beetles were collected from rodent hosts during the winter months than during the summer months, Rüschkamp (1914) suggested that it was quite possible that the beetles were hibernating with the rodent host. However, following a more extensive study of this species he finally concluded that *L. testaceus* was a "true parasite" of certain rodents (*Arvicola terristris* L., *A. amphibius* L., *Apodemus sylvaticus* L., and *Clethrionomys glareolus* Schreber), perhaps feeding on dermal scales and other skin debris, for at least a part of the adult life. The finding of the adults of *L. testaceus* in bumble bee nests was considered exceptional since none were ever found in the nests examined by him during the course of his ten-year study of the species. He further considered the larvae to be scavengers, living in the nesting debris of the host of the adult (Rüschkamp, 1921).

A recent citation (Buck, 1951) concerning the recovery of this species from the nest of a barn owl (*Tyto alba* Scop.), brought to our attention by E. A. Hicks (*in litt.*), is believed by the latter to represent an example of "faunal contamination resulting from the feeding habits of the owl."

In summary, it would seem most logical to assume that the beetle is primarily an ectoparasite of its recorded rodent and insectivore hosts. However, this relationship does not appear to be obligatory, since beetles separated from their hosts seem capable of prolonged survival. The records from the nests of wild bees probably represent recoveries of individuals which were removed from their rodent or insectivore host during a feeding-raid upon the bee nests.

A considerable amount of confusion has arisen concerning the identity of *L. testaceus* in the Nearctic region. It has been considered a Holarctic species and *Leptinus americanus* Leconte described from Iowa as well as *Leptinus caucasicus* Motsch. described from Russia have fallen into synonomy.

Werner and Edwards (1948), after examining a series of leptinids taken from shrews in New York, discovered that there were significant morphological differences between their series and the illustrations given for *L. testaceus* by Jeannel (1922) and by Sharp and Muir (1912). When the genitalia were examined and compared with these illustrations and also with European material, it was found that a great disparity existed. Examination of Leconte's types revealed

FIG. 1

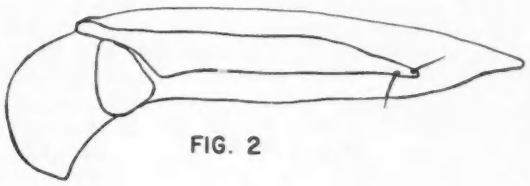

FIG. 2

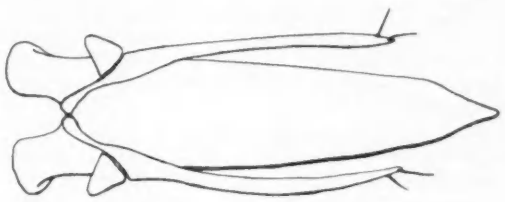

FIG. 3

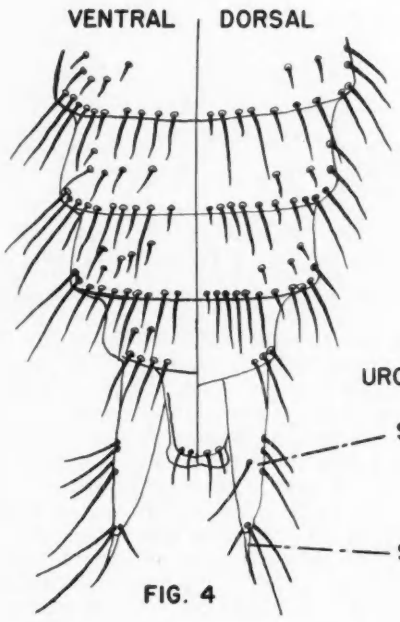

FIG. 4

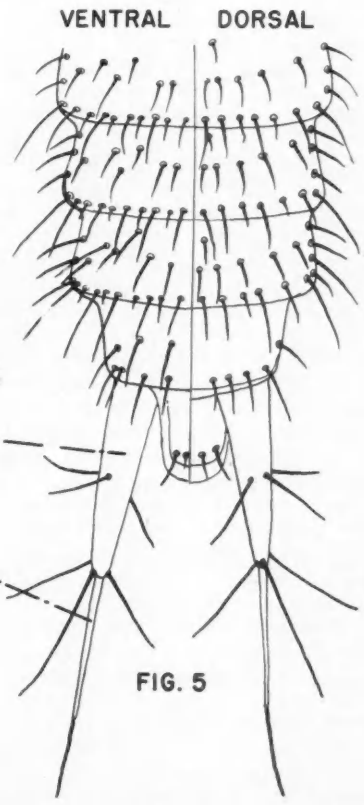

FIG. 5

FIGS. 1–4. *Leptinillus validus*. 1. Ventral and dorsal aspects of head of larva; 2, 3, lateral and dorsal aspects of male genitalia; 4, ventral and dorsal aspects of abdominal segments 6–10 of larva. FIG. 5. *Leptinus americanus*. Ventral and dorsal aspects of abdominal segments 6-10 of larva. FIGS. 1 and 4 drawn from material collected at Sebeois, Penobscot County, Maine and made available through the courtesy of R. E. Olson. FIGS. 2 and 3 drawn from Minnesota material. FIG. 5 drawn from material collected at Brookland, D. C. FIGS. 4 and 5 not drawn to the same scale.

that they were all females; however, it was found that the females of the New York series compared perfectly with Leconte's material, and consequently the specimens were assigned to *L. americanus*. It was also stated that most or all of the specimens from Eastern North America may be referable to this later species. Jeannel stated (1922) that leptinids obtained from Mammouth Cave, Kentucky were found to be identical with European specimens. However, in view of the gross similarity of these two species as observed by Werner and Edwards, it is possible that a misdetermination could have been made by Jeannel.

Apparently the larva of *Leptinillus validus* has never been described. When we attempted to compare this larva with illustrations of *Leptinus testaceus* in Böving and Craighead (1930) and Peterson (1951), we found certain discrepancies in their drawings which prompted us to write the United States National Museum for the material used by these authors. Slide mounted material used by the previously mentioned investigators was made available to us through the courtesy of Dr. E. A. Chapin. Additional unmounted material consisting of larvae, pupae and two adults collected from a mole's nest in the District of Columbia by T. H. Scheffer was also made available to us from this same institution. The genitalia of the one male adult in this material are identical with the genitalia of *L. americanus* illustrated by Werner and Edwards.

Therefore, we also conclude that *L. americanus* is a valid species and that it is quite likely that most references to *L. testaceus* in the Nearctic region are referable to *L. americanus*. These larvae agree with the slide mounted material apparently used by Böving and Craighead and Peterson. Therefore, the illustrations of *L. testaceus* appearing in papers by these authors are what we choose to call illustrations of *L. americanus*. It should be pointed out that larvae of *L. testaceus* are unavailable to us at this time, and apparently no illustration of the larva exists.

The known larvae of the Nearctic species (*Leptinus americanus* and *Leptinillus validus*) can be differentiated by the characters of the urogomphi. The urogomphi are two segmented in both species; however, in *L. validus* the distal segment is quite short in relation to the basal segment. The distal segment bears a terminal seta as long as or slightly longer than the segment (Fig. 4). The distal segment of the urogomphus of *L. americanus* is three-fourths the length of the basal segment. The distal segment bears a terminal seta which is about one-half the length of the segment (Fig. 5). The setation of the posterior sclerites of the abdomens of the two species differs especially on the tergites. The larvae of *L. validus* are larger and more robust than those of *L. americanus*.

Inasmuch as references to this family are somewhat scattered, and since the only synopses of the family appear in foreign journals (Jeannel, 1922, and Olsufiev, 1923), the following synopsis prepared from the literature and our data might be useful to American workers.

Leptinus testaceus Müller

1817, in Germar, Mag. Ent. 2: 268 (Cited from Junk and Schenkling, 1911–1913)

The range of this species has been believed to be Holarctic; however, it is not unlikely that it is restricted to the Palearctic region. Its recorded hosts are rodents (Family Muridae) and insectivores (Family Soricidae). The records from the nests of wild bees and of birds are considered exceptional. The larvae, which have been found only in nesting debris, are believed to be scavengers.

The characters of the adult beetle are figured by Jeannel, 1922 figures 1–16. The larva is not figured to our knowledge. The male genitalia are figured by Jeannel, Figures 14, 15 and 16; and by Sharp and Muir, 1912, plate 51, Figures 55 and 55a.

Leptinus caucasicus Motschoulsky

1840, Bull. Soc. Nat. Mosc., 13: 176, pl. 4, Fig. H. (Cited from Jeannel, 1922).

This species has been synonomized with *L. testaceus* (cf. Junk and Schenkling, 1911–1913, page 155).

Leptinus americanus Leconte

1866, Proc. Acad. Nat. Sci. Philadelphia, 1866: 367.

This species has been synonomized with *L. testaceus* but was removed from synonomy by Werner and Edwards (1948). The range of the species is not definitely known. The types, all females, were found under a log in a "mouse nest" at Keokuk, Iowa. The specimens examined by Werner and Edwards taken from *Blarina brevicauda talpoides* from several localities in New York, the male recovered from *Blarina brevicauda carolinensis* in Alabama cited by Royal (1952), and the specimens examined by us from the District of Columbia are the only positive records known to us. It is quite possible that references to *L. testaceus* in the Nearctic region are referable to *L. americanus*.

The characters of the imago and the male genitalia are figured by Werner and Edwards. The characters of the urogomphi and the terminal abdominal segments of the larvae are figured in this paper.

Leptinus seriatus Dodero

1916, Ann. Musc. Civ. Stor. Nat. Genova, 47: 347 (Cited from Jeannel, 1922).

According to Jeannel (page 587) this species was described from a single female taken from leaf-mould in the woodland of Mount Rose near d'Alagna, Italy. Jeannel questions the validity of the species, suggesting that it may be only an abnormal individual of *L. testaceus*.

Leptinus vaulogeri Jeannel

1922, Arch. Zool. Exp. Gen., 60: 587.

This species was described from specimens taken in Algeria, Africa, and Jeannel states that it is quite likely that *L. vaulogeri* replaces *L. testaceus* in this region. The specimens were taken from the nest of *Apodemus sylvaticus* (L.).

The larva is unknown and the male genitalia are described but not figured. The characters of the adult are figured by Jeannel on plates 32–36.

Leptinillus validus Horn

1872, Trans. Amer. Ent. Soc. 4: 145.

The range of this species is Nearctic and is probably coincident with that of *Castor canadensis*.

The finding of the larvae and imagoes in the fur of the beaver host would suggest a relationship tending toward obligate parasitism. The only recorded host is *Castor canadensis*.

The characters of the adult are figured by Horn (1883, plate 5, Figures 1–6). The head of the larva, the characters of the urogomphi and the abdominal segments, and the male genitalia are figured in this paper.

Leptinillus aplodontiae Ferris

1918, Can. Ent. 23: 125.

The range of this species is probably coincident with that of *Aplodontia* sp. (*rufa* ?), its only recorded host. Ferris believes it to be an ectoparasite.

The male genitalia together with some of the characters of the imago are figured by Ferris and by Bugnion and du Buysson (1924). The larva is unknown.

Silphopsyllus desmanae Olsufiev

1923, Rev. Russ d'Ent. 18: 81.

Recorded only from the "water rat" *Desmana moschata* L., an insectivore indigenous to European Russia, taken from the River Sura, near Penza, Russia and from the River Matyra in the District of Liptzk, Russia.

The male genitalia are undescribed. The larva is described by Semenov-Tian-Shansky and Dobzhansky (1927).

SUMMARY

Information gained through correspondence indicate that the range of *Leptinillus validus* is coexistant with that of the beaver *Castor canadensis*. There is favorable evidence based upon morphological characteristics and known habits to indicate that this beetle is an ectoparasite of the beaver.

Additional identifications of *Leptinus americanus* Lec. substantiate the recent removal of this species from the synonomy of *Leptinus testaceus* Müller by Werner and Edwards. It is suggested that *L. americanus* replaces *L. testaceus* in the Nearctic region.

The knowledge of the other members of this family is reviewed.

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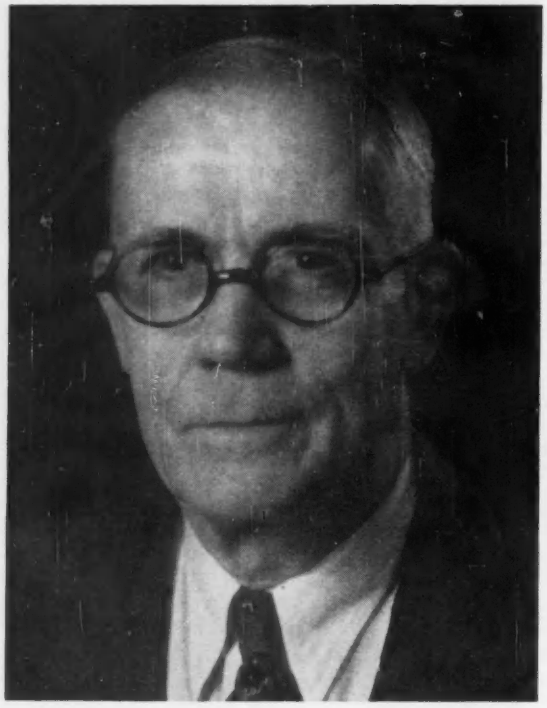
OBITUARIES

Raymond Carroll Osburn

1872–1955

Dr. Osburn was born January 4, 1872 on a farm in Licking County near Newark, Ohio. Due to certain physical handicaps he was deprived of much of the formal school experiences. In these early formative years his mother taught him, giving him the necessary background from which to ascend to heights of understanding through prodigious reading and his infatuation for the facts of nature that he gleaned from woods and fields of the



countryside in which he spent his youth: With this uncommon substitute for formal training he entered Ohio State University as a special student at the age of 23. It was not long, however, before he earned for himself regular academic standing and was given the Bachelor of Science degree in 1898. After graduation he taught classes at Starling Medical College and gained the Master of Science degree from his Alma Mater. With this he went to Fargo College, North Dakota, and then to Columbia University to earn his Doctor of Philosophy degree in 1906. While at Fargo he met Miss Mary Hubbell one of his students whom he later married on August 19, 1903.

He also held such positions as Assistant Professor at Barnard College of Columbia University, Professor and head of the Biology Department of the Connecticut College for Women, Scientific Investigator for the U. S. Bureau of Fisheries, and Associate director of the New York Aquarium.

When Professor Herbert Osborn retired from the chairmanship of the Department of Zoology and Entomology the university looked about for an outstanding candidate for the place. It was Raymond Osburn whom they chose to hold this post for 25 years. This was a period of rapid growth for the University and splendid expansion of the Department under his guidance.

For 20 years he guided the destinies of the Franz Theodore Stone Laboratory at Put-in-Bay, Ohio, and largely through his efforts the University acquired possession of Gibralter Island with the generosity of Mr. Julius Stone. Dr. Osburn was a member of the national honorary Society of Sigma Xi and held membership in 15 scientific societies. Early in his career he was sent by the American Museum of Natural History to study the aquatic life of the Caribbean Sea. Bryozoa, fishes and insects were his chief groups of interest on which he published many papers. Such was his repute that after retiring from the chairmanship of his Department he was called to California to work on the collections of Bryozoa made by the Hancock Foundation expeditions in Pacific waters from Alaska to Peru. As a result he prepared three noteworthy volumes on his studies. For the excellence of one of these he was awarded the Daniel Giraud Elliot 1950 gold Medal by the National Academy of Science. In 1949 the Ohio State University awarded him the honorary degree of Doctor of Science.

Dr. Osburn lived and practiced a philosophy of life that is nowhere better shown than in the volume of 165 letters sent to him at his retirement containing such expressions as:

". . . your kind and sympathetic attitude has constantly been an inspiration to me."

". . . The kindness of the man himself, his comprehensive soul, his deep, unerring instinct as to each person's goal."

"Sir, I salute you, great teacher, perfect gentleman, naturalist of the old school, and, above all, a true friend."

He lived as he expressed it in a few lines which he himself wrote as he contemplated his retirement:

"What pleases me most, looking back o'er the years,
As the time for retirement now rapidly nears,
Is the progress of students I've worked with, and on,
As out to the world and its work they have gone.
And I like to think, maybe, I've had a small part
In giving a fine bunch of men a good start.
For a teacher there can be no greater reward,
Though his days may be long and his labors be hard,
Than noting the heights which his students attain,
And feeling his efforts have not been in vain."

Dr. Osburn died August 6, and was buried August 9, near his birthplace at Newark, Ohio.

D. F. MILLER

Charles Thomas Brues, II.

1879–1955.

Charles Thomas Brues, Emeritus Professor of Entomology, Harvard University, passed away on July 22, 1955, at Crescent City, Florida. He had been on the Harvard staff for 46 years.

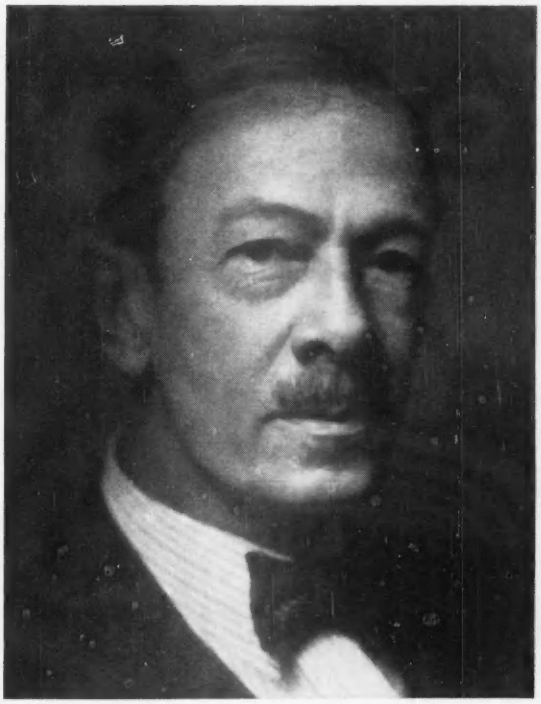
My acquaintance with Brues began in 1893, when his family moved to Chicago from Wheeling, West Virginia.

He and I struck up a friendship which continued for 62 years. When we entered high school we expected to specialize in chemistry, but entomology proved more exciting, and under the guidance of Principal O. S. Westcott and our biology teacher, H. E. Walter, we acquired a specialist's knowledge of insects.

We had prepared to enter Chicago University, but on the way to matriculate we met Dr. W. M. Wheeler who advised us to go with him to the University of Texas where he had just accepted the headship of the zoology department. At Texas we wrote several joint papers, the Chemical Nature of some Insect Secretions, and New Species of Dolichopus and Hygroceleuthus, as well as others with single authorship. After a year we were given scholarships and later a class in entomology. On leaving Texas Brues went to Columbia University since his family had moved to New York, and I to Chicago University. A year later Brues accepted appointment in the U. S. Department of Agriculture at Paris, Texas, where he married Beirne Barrett, a student majoring in zoology at Texas. Two children resulted from this marriage, Dr. Austin Brues and Dr. Alice Brues.

Following his marriage Brues accepted a position as Curator of Invertebrates at the Milwaukee Public Museum, and in 1909 he was appointed Instructor in Entomology at Harvard University to work again under Dr. Wheeler who had been appointed Dean of the graduate school at the Bussey Institution of Harvard. Going through the successive grades, Assistant Professor 1912, Associate Professor 1926, Professor 1935 and Emeritus 1946, he published some 200 papers on insects. His early love was for the Phoridae and the parasitic Hymenoptera, but a glance at his publications shows much diversity: fossil Hymenoptera, Peripatus, Insects of hot springs, Insects and human welfare, and Insect Dietary; an account of the food habits of insects. He was joint author with me of a Key to the Families of North American Insects (1915) and the Classification of Insects (1937), the greatly expanded revised edition appearing shortly before his death. He was Editor of Psyche since 1909. He participated in exploratory trips to the West Indies in 1910, 1912 and 1926, to South America in 1913, to the Dutch East Indies in 1937, to the Hudson Bay region in 1945, and to the Phillipines in 1949.

Brues was Fellow in the American Academy of Arts and Science, the American Association for Advancement of Science, the Entomological Society of America (president, 1929), and member of the American Association of Economic Entomologists, the Cambridge Entomological Club, American Society of Naturalists, the



Boston Society of Natural History, the Chicago Academy of Science, The Florida Academy of Science, and the Florida Entomological Society.

AXEL LEONARD MELANDER

THE EVOLUTION AND TAXONOMY OF THE SARCOPHAGINAE (DIPTERA, SARCOPHAGIDAE), by SELWYN S. ROBACK. Illinois Biological Monographs, vol. 23, nos. 3–4. Pp. v + 181, 34 plates (460 figs), 9 charts. 1954. Price, $4.00; cloth, $5.00.

No student of the muscoid flies, and in particular of the Sarcophagidae and related families, can afford to overlook this contribution to the taxonomy and phylogeny of the group. To date, there has been no satisfactory classification of the Sarcophaginae. The major problem, as the author remarks, has been the delineation of genera, and the success of such a delineation must depend upon an understanding of phylogenetic relationships. In order to move in this direction, Dr. Roback has postulated a sarcophagine archetype and has attempted to derive a family tree from such a basis. His classification, resulting from such a phylogeny, has been based largely on male genitalic structures, and particularly the morphology of the aedeagus. He freely admits the preliminary nature of the study, and expresses hope that light may be shed on the subject from the consideration of the female genitalia, biology, and immature stages.

In view of the restricted approach, the title seems to too broad. Also, the user of the work should be cautioned about omissions, particularly of many of the generic names proposed by Townsend. If the author considered these of no validity, he should have so stated, since Townsend's "Manual of Myiology" has become so standard a tool for workers in this area. Finally, the author handles scientific names very carelessly; many are misspelled, and some species are attributed to the wrong author or given the wrong date. These remarks are not made to detract from the worth of the work, but to caution the beginner against accepting it too uncritically.—MAURICE T. JAMES.

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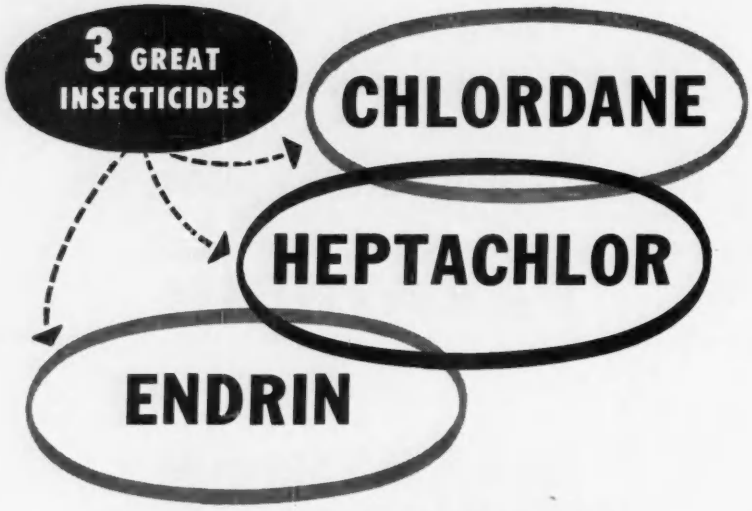

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